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An Anomalous Bedding/Cleavage Relationship

Abstract

In a major fold in the Kootenay arc belt in N.E. Washington, the F_1 fold geometry can be mapped from the bedding/cleavage relationships, even though the fold has been refolded by later crenulation folds. The early cleavage, S_1, is preserved in the psammitic units of the Lower Cambrian Maitlen Phyllite. However, anomalous bedding/cleavage relationships are recognized in some outcrops in which the later folding has locally reversed the angular relationship between the S_1 cleavage and the bedding. The S_1 cleavage appears to have been the dominant anisotropic control on the F_2 folding, rather than the bedding, which appears to have behaved as a relatively passive marker.

One of the most important relationships used by structural geologists to map fold structures is the angular relationship between bedding and axial plane cleavage which allows one to determine the position of an outcrop in a fold (e.g., Wilson, 1961; Ramsay, 1967, fig. 7-77). In a hinge zone, the cleavage will be at a high angle to the bedding, whereas in the limb zones, the cleavage will be at a low angle to the bedding. There will be a different sense of the cleavage crossing the bedding on opposite limbs of the fold.

Even in areas that have been refolded, the general sense of the early bedding/cleavage relationships is often maintained. The angular relationships of the early bedding/cleavage may be modified by the later deformation (e.g., Ramsay, 1967, figs. 9-16, 9-32); but usually the general position within the early fold can still be delineated.

However, during the course of detailed mapping in the Kootenay Arc in N.E. Washington, we have come across examples of anomalous bedding/cleavage relationships. The structure of the Lower Cambrian Quartzite (Gypsy) and Maitlen Phyllite just south of Northport (Stevens County, N.E. Washington) consists of a large over-turned anticline facing towards the northwest and plunging to the southwest (Mills and Nordstrom, 1973). The fold and associated minor parasitic folds have a pervasive axial plane cleavage. Later folds, F_2, also plunging southwesterly, have refolded the early folds and have formed a crenulation axial plane cleavage in the more phyllitic units. In most outcrops of the quartzitic units, the position within the early fold can be discerned because the early cleavage is preserved within the bedding. The sense of the bedding/cleavage is largely unaffected by the later crenulation. An example is shown in Figure 1 of a quartzitic unit within a phyllite matrix. The phyllite is crenulated and has an incipient crenulation cleavage, axial planar to the minor fold. The minor fold affects both the bedding and the early axial plane cleavage, which cuts through the bedding at a very low angle. The sense of the S_1 cleavage crossing the bedding is maintained around the later fold, and shows the early fold to be closing anticlinally to the southeast.

In contrast, Figure 2a shows a quartzitic unit within a quartzitic phyllite matrix. It

Figure 1. Minor F_2 fold in a quartzite layer, viewed down plunge, towards the southwest. First cleavage, S_1, is folded with bedding, S_0, but retains the original bedding/cleavage sense around the fold. Cleavage crosses bedding from upper left to lower right indicating an anticlinal closure to the southeast.

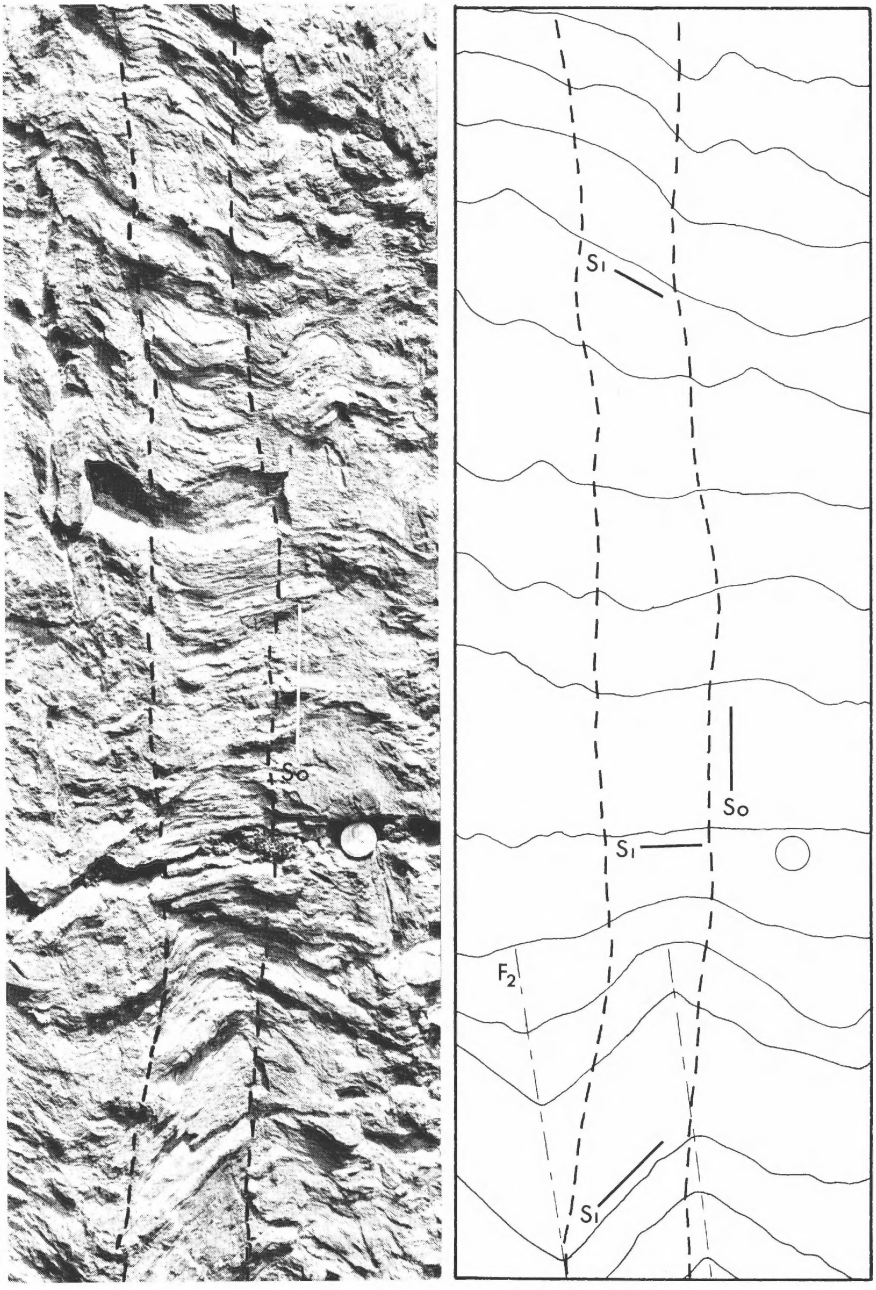

Figure 2a. Progressive change of bedding/cleavage sense along a quartzitic unit. Axial traces of F_2 folds cross bedding at a low angle. The S_1 cleavage is folded but the bedding, S_0, is largely unaffected. The folds characteristically die out along their axial traces. Figure 2b. Line drawing of Fig. 2a, showing the bedding, S_0, the first cleavage, S_1, and the F_2 fold axial surface traces.

can be seen that the angle between the bedding and the S_1 cleavage changes along the bedding from an acute angle, up to ninety degrees, then to an acute angle facing the opposite way.

A first interpretation is to suggest that this outcrop represents a minor first fold that has been flattened out or unfolded by the later deformation. However, further examination of the outcrop reveals that the cleavage is folded into a series of chevron folds, which change amplitude along their axial plane traces, locally dying out into planar S_1 surfaces. The bedding unit traverses the chevron folds at a low angle to their axial surface traces. Therefore, in places it follows one limb of the chevrons, gradually moves into a hinge zone and eventually onto the opposite limb; thus the angle of the cleavage to the bedding gradually changes. This geometry results in areas of anomalous or locally reversed bedding/S_1 cleavage relationships. It is not possible to ascertain the original angle between the bedding and the cleavage before the later folding. Nor is it possible to determine the original sense of the cleavage crossing the bedding, although from the areal context, this outcrop is known to be on the northwest limb of the major anticline. The bedding/cleavage sense in the lowermost portion of Figure 2a would then be consistent with the position of the outcrop within the major fold.

In this chevron folding example, the bedding appears to have very little mechanical control on the folding, behaving as a passive marker stripe, with the early cleavage acting as the dominant anisotropy.

It is not possible to ascertain the mechanical effect of the bedding units in the example shown in Figure 1. The bedding is at a very close angle to the cleavage and it is therefore difficult to know whether one or both controlled the folding. The thickness of the bedding presumably influenced the wavelength of the fold, as smaller wavelength folds are developed in the thinner bedding unit in the left side of the photo. The smaller wavelength may, of course, be due to there being fewer quartzitic cleavage "microlithon" units in the thinner quartzitic unit.

Conclusion

As long as careful observations are maintained, the anomalous bedding/cleavage relationships can usually be recognized and so taken into account when mapping out early structures by bedding/cleavage relationships in a refolded area. In this particular area at Northport, there is also a well established stratigraphy and therefore stratigraphic control on the mapping besides the bedding/cleavage relationships. There may, of course, be some occasional isolated outcrops in which not enough of the folding can be observed to recognize the anomalous situation and which will therefore give misleading information about the first fold geometry.

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Vegetation of Steep Slopes in the Shrub-Steppe Region of Southcentral Washington

Abstract

This paper describes the vegetation and soil on steep natural slopes of ten ravines along the Columbia River in southcentral Washington. Total vegetative cover averaged 25 percent on the south-facing and 71 percent on the north-facing slopes. The mean number of species was significantly higher on the north slopes, but neither Shannon's nor Simpson's diversity indices showed significant differences. Four species were restricted to south slopes and ten were restricted to north slopes. *Poa sandbergii* and *Agropyron spicatum*, native perennial bunchgrasses, dominated the plant cover on north-facing slopes and *Bromus tectorum*, an alien annual grass, dominated south-facing slopes. Soils were shallow and stony on the south-facing slopes.

Introduction

Canopy cover and species composition of undisturbed vegetation of the shrub-steppe region of southcentral Washington have been described by Daubenmire (1970) but, for the most part, these descriptions are of stands on level to gently sloping land. Descriptions of vegetation on steep slopes are scarce (Dillon, 1967; Rickard, 1976). The purpose of this paper is to present canopy cover and species composition data taken on steep slopes along the Columbia River.

Differences in vegetation on steep slopes have long been recognized and related to microclimate. Few species seem totally restricted to a particular slope aspect but appear to respond to microclimatic differences with shifts in density (Cantlon, 1953). Microclimate is in turn influenced by vegetative cover (Ayyad and Dix, 1964). Steep south slopes had higher soil and air temperatures than north slopes (Rickard *et al.*, 1971; Rickard *et al.*, 1973). Slope-induced differences in solar radiation caused changes in primary production, protein content, and root-shoot ratios in cheatgrass (*Bromus tectorum*) (Hinds, 1975).

The study sites were located on the eastern bank of the Columbia River, Franklin County, Washington, approximately 16 km (10 mi) north of the city of Pasco. Steep bluffs representing the eroded face of the Ringold formation rise 30-60 m (100-200 ft) above the Columbia River. Deep ravines have been eroded into the face of the bluff; the ravines run east and west so that the walls of the ravines provide contrasting north- and south-facing exposures of similar steepness and similar geologic strata. The walls of the ravines are steep, ranging between 30 and 40° (58 and 84 percent).

The regional climate is characterized by low precipitation, averaging slightly less than 180 mm (7 in) annually, nearly all of which falls in the cool part of the year. Sum-

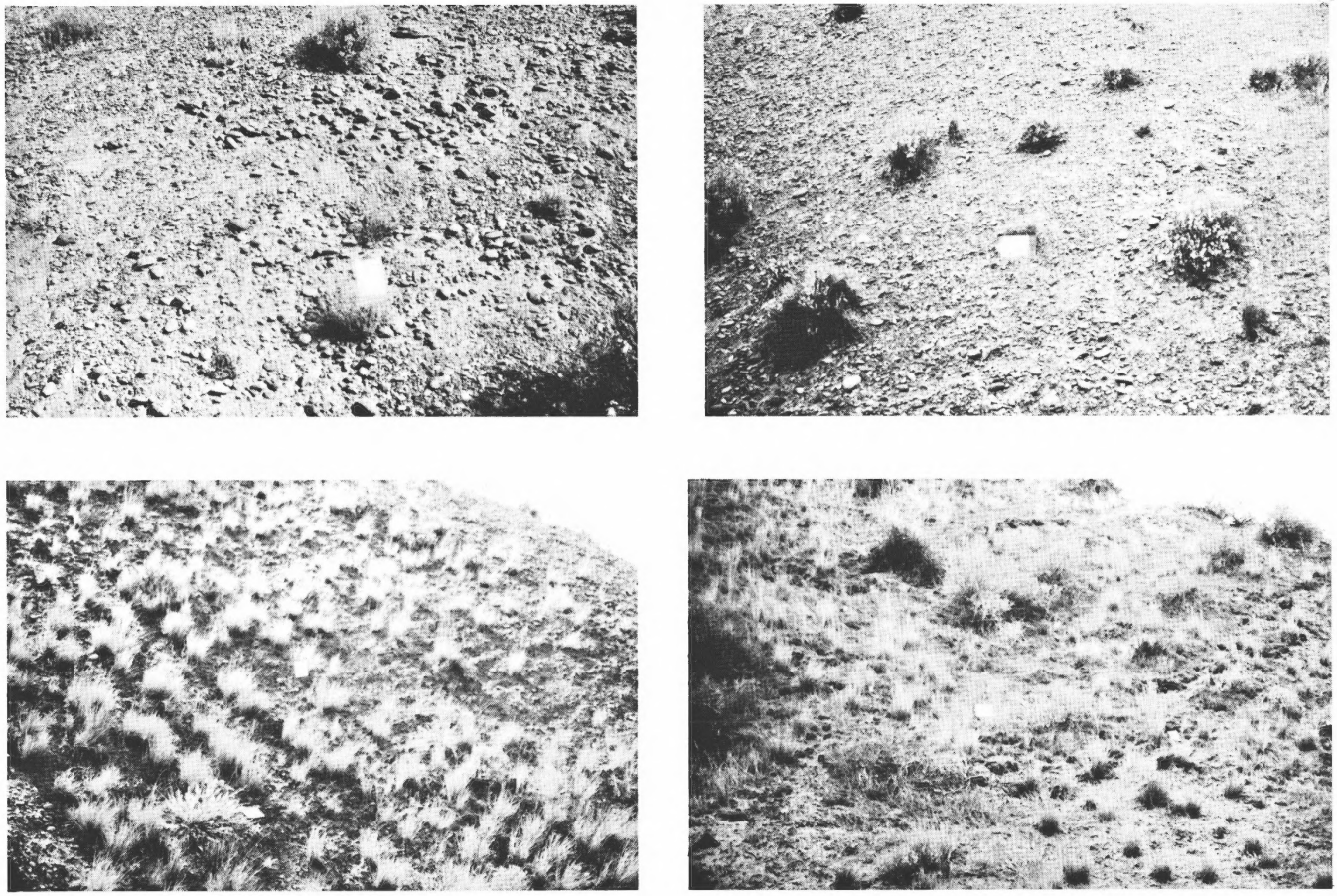

Figure 1. Photographs of two ravine walls to show contrasting vegetation. Top two are south-facing slopes and bottom two are north-facing slopes. Each pair is from the same ravine.

mers are hot and dry and winters cold to cool and wet. The ravines seldom carry surface water runoff.

Methods

Ten ravines large enough to avoid local ridge and valley effects were selected (Fig. 1). In each ravine, two 3 x 4 m plots were set out midway between rim and the valley bottom, one on the north and one on the south slope. Samples of the surface 5 cm of soil were taken just outside the lower left-hand corner of each plot. Soil depth measurements and canopy cover estimates were taken at 0.5 m intervals along the length of the two sides (3 m) and bottom (4 m) of each plot for a total of 23 cover estimates and soil depth measurements per slope. Soil depth was estimated by pushing a metal rod vertically into the soil until it met a solid resistance, usually a rock. Canopy cover was estimated using the Daubenmire (1959) method with a 20 x 50 cm frame.

The percent cover on each slope was converted to proportional cover by dividing each value by the total. The proportional cover was used to calculate diversity indices according to Hill (1973):

$$N_a = (p_1^a + p_2^a + p_3^a \cdots + p_n^a)^{1/(1-a)}$$

where N_a is a diversity index, $p_1 \cdots p_n$ is the proportional cover, n is the number of species, and a determines the diversity index:

$a = 0$, Number of species

$a = 1$, exp H (H is Shannon's entropy)

$a = 2$, reciprocal of Simpson's modified index

For $a = 1$,

$$N_1 = \exp\left(-\sum_{i=1}^{n} p_i \ln(p_i)\right) = \exp(H) \qquad \text{(Hill, 1973)}$$

Wilcoxon's Signed Rank Test was used to test for differences in percent cover for each species, total cover, and the diversity indices, because it assumes only that the samples come from the same but unknown distribution (Woolf, 1963).

The soil samples were analyzed for percent gravel (larger than 2 mm); percent sand, silt, and clay; percent organic matter; electrical conductivity; and pH. The percent rock is separate from the percent sand, silt, and clay. The 10 values from each slope aspect were averaged to characterize the chemical and physical soil properties.

Results and Discussion

Thirty-seven species were recorded from twenty slopes (Table 1). Of these, 23 were common to both slopes, four were found only on the south slopes, and ten were found only on the north slopes. *Descurainia pinnata, Plectritis macrocera, Agropyron spicatum, Draba verna,* and *Poa sandbergii* were found on at least nine north slopes. *Cryptantha circumscissa* was found on at least nine south slopes. Only *B. tectorum* was found on all slopes examined. *Agropyron spicatum, Poa sandbergii, Draba verna, Holosteum umbellatum,* and *Plectritis macrocera* were better represented on the north slopes and *Bromus tectorum, Festuca octoflora,* and *Gilia leptomeria* were better represented on the south slopes. The south slopes ranged from 4.7 to 58 percent cover, whereas the north slopes ranged from 43 to 98 percent (different at $p<0.01$) (Table 2). The south slopes had much less cover (25 percent) than the north slopes (71 percent), due to grasses (S: 14

TABLE 1. Mean canopy cover (X), standard errors (SE), and frequency (F) of each species. Wilcoxon's Signed Rank Test used to determine differences at $p < 0.05$ (*) and $p < 0.01$ (**). Means and standard errors are descriptive only and were not used in tests for significant differences.

Species	South Facing			North Facing		
	F	SE	X	X	SE	F
Grasses						
Perennial						
****Agropyron spicatum**	0.3	0.17	0.20	13.66	1.68	1.0
Poa cusickii	0	0	0	5.98	3.69	0.4
****Poa sandbergii**	0.5	0.24	0.50	28.11	4.52	1.0
Total perennial grasses*		0.29	0.70	47.75	6.07	
Annual						
***Bromus tectorum**	1.0	4.70	13.80	7.72	2.91	1.0
***Festuca octoflora**	0.3	0.06	0.09	0.34	0.11	0.5
Total annual grass		4.70	13.89	8.06	2.91	
Total Grasses*		4.71	14.59	55.81	6.73	
Forbs						
Perennial						
Achillea millefolium	0.1	0.01	0.01	0.65	0.41	0.3
Astragalus purshii	0.3	0.19	0.32	0	0	0
Balsamorhiza careyana	0.1	0.60	0.60	0.39	0.37	0.3
Calochortus macrocarpus	0	0	0	0.23	0.19	0.2
Crepis atrabarba	0	0	0	0.02	0.01	0.2
Delphinium sp.	0	0	0	0.97	0.57	0.4
Fritillaria pudica	0	0	0	0.01	0.01	0.1
Lithospermum ruderale	0	0	0	0.21	0.13	0.3
Lomatium grayii	0.6	1.03	2.27	0.07	0.07	0.1
Lomatium macrocarpum	0.1	0.01	0.01	0.84	0.41	0.5
Phlox longifolia	0	0	0	0.17	0.15	0.2
Total perennial forbs		1.21	3.21	3.56	0.94	
Annuals						
Amsinckia lycopsoides	0.6	0.16	0.24	0.12	0.10	0.3
***Cryptantha circumscissa**	0.9	0.23	0.90	0.11	0.07	0.4
Descurainia pinnata	0.8	0.18	0.48	0.65	0.21	1.0
****Draba verna**	0.1	0.04	0.04	1.15	0.28	0.9
Epilobium paniculatum	0.2	0.01	0.02	0.01	0.01	0.1
***Gilia leptomeria**	0.6	0.10	0.30	0.02	0.01	0.2
****Holosteum umbellatum**	0.1	0.01	0.01	3.59	1.24	0.8
Layia glandulosa	0.2	0.02	0.03	0	0	0
Lactuca serriola	0.4	0.20	0.24	0.26	0.13	0.5
Mentzelia albicaulis	0.3	0.04	0.07	0	0	0
Microsteris gracilis	0.4	0.11	0.22	0.51	0.16	0.8
Montia sp.	0	0	0	0.10	0.10	0.1
Phacelia sp.	0.4	0.10	0.17	0.01	0.01	0.1
****Plectritis macrocera**	0.4	0.20	0.25	2.23	0.89	0.9
Sisymbrium altissimum	0.2	0.01	0.02	0.13	0.10	0.2
Total annual forbs*		0.48	2.99	8.89	1.59	
Total Forbs*		1.30	6.20	12.45	1.85	
Shrubs						
Artemisia tridentata	0	0	0	0.07	0.07	0.1
Chrysothamnus nauseosus	0	0	0	0.30	0.30	0.1
Eriogonum niveum	0.3	0.50	0.71	0	0	0
Eriogonum sp.	0.3	0.61	0.84	0.59	0.59	0.1
Grayia spinosa	0.1	0.01	0.01	0.74	0.49	0.2
Salvia dorrii	0.4	1.24	2.62	1.09	1.02	0.2
Total Shrubs		1.47	4.18	2.79	1.31	
TOTAL COVER ALL SPECIES*		5.10	24.97	71.05	7.10	

percent, N: 56 percent) and forbs (S: 6 percent, N: 12 percent). Shrubs had similar cover percentages on the two slope aspects.

Dominance, as indicated by canopy cover, was restricted to a few species. On the south slopes, *B. tectorum* provided most of the cover, whereas on the north slopes *A. spicatum*, *P. sandbergii*, and *B. tectorum* provided most of the cover. Individual plants were often

TABLE 2. Percent cover and diversity indices (see text for explanation of N_0, N_1, and N_2). Wilcoxon Signed Rank Test used to determine differences at $p < 0.05$ (*) and $p < 0.01$ (**). Means and standard errors are descriptive only and were not used in tests for significant differences.

	Slope Number											Standard
	1	2	3	4	5	6	7	8	9	10	Mean	Error
South Facing Slopes												
Percent Cover**	9.1	4.7	58.4	29.0	20.8	29.5	37.4	8.4	26.4	25.5	24.9	5.0
N_0*	9.0	6.0	6.0	11.0	13.0	12.0	10.0	11.0	13.0	9.0	10.0	0.8
N_1	5.3	3.7	1.6	4.2	6.1	5.7	4.1	6.2	3.0	4.1	4.4	0.5
N_2	4.2	2.9	1.3	3.0	4.7	4.0	2.6	4.4	2.0	3.5	3.3	0.4
North Facing Slopes												
Percent Cover**	64.2	63.7	87.5	69.5	97.8	98.3	79.3	71.6	45.4	42.9	72.0	6.1
N_0*	12.0	13.0	16.0	16.0	12.0	21.0	9.0	14.0	12.0	11.0	13.6	1.1
N_1	4.9	4.7	7.0	6.5	3.7	8.5	3.8	5.4	3.8	4.5	5.3	0.5
N_2	3.8	3.1	5.0	4.3	2.4	6.1	2.8	4.0	2.4	3.4	3.7	0.4

widely spaced and occurred on few slopes, yielding low frequency (F) values (Table 1).

The diversity indices calculated from these data are shown in Table 2. The number of species (N_0) ranged from 6 to 13 on the south slope, and on the north slope from 9 to 21. The means for N_0 were different at $p<0.05$. The value N_1 (exp (H), where H is Shannon's entropy), ranged from 1.6 to 6.2 on the south slopes and 3.7 to 8.5 on the north slopes. The means for N_1 for the two slope aspects were not different. The value N_2 (reciprocal of Simpson's modified index) ranged from 1.3 to 4.7 on the south slopes and 2.4 to 6.1 on the north slopes. The means of N_2 were not different.

Average soil depth (Table 3) (penetrability) on the north-facing slopes (32.9 cm) was 3.8 times greater than on the south-facing slopes (8.6 cm) (significant at $p<0.05$). South-facing slopes were stonier and also had more sand and less silt and clay (Table 3). Organic matter content was slightly higher on the north-facing slopes and pH was slightly lower. Soluble salt content (as indicated by electrical conductivity values) was not different between the two slope aspects.

TABLE 3. Soil properties of steep north and south slopes. Significant differences based on t-test $p < 0.5$ (*) and $p < 0.01$ (**).

Soil Properties	South Facing Mean	South Facing Standard Error	North Facing Mean	North Facing Standard Error
*Soil depth (vertical) cm	8.6	1.0	32.9	7.0
**Rock %	53.3	5.6	14.5	5.0
Sand %	65.4	2.2	57.2	7.7
Silt %	31.8	2.5	39.0	3.2
Clay %	2.8	1.1	3.8	1.1
Organic Matter %	0.5	0.1	1.1	0.1
pH	7.7	0.1	7.5	0.1
Conductivity mmhos/cm	0.34	0.06	0.36	0.03

Diversity is a measure of how many species are present as examination proceeds down to a certain level of rarity (Hill, 1973). On the south slopes *B. tectorum* alone was the dominant species, whereas on the north slopes, dominance was shared by *B. tectorum*, *P. sandbergii*, and *A. spicatum*. However, the estimates of the number of dominant species (N_1 and N_2) were not different, suggesting that the one abundant species

on the south slope, *B. tectorum*, is equivalent in dominance to the three co-dominant species on the north slopes. With more consideration of rare species as given in the N_1 diversity values, the north slopes have slightly more (S: 4.4, N: 5.3) species though the difference is not statistically significant. Overall, dominance, as indicated by N_1 and N_2, appears the same.

Seasonal differences in microclimate may account for the dissimilar number of species (N_0). A major difference between slope aspects is the length of time soil water is available when temperatures are conducive to growth. The thin soil on the warm south slopes holds less water and dries faster than the soil of the north slopes. Perhaps fewer species can complete their life cycle in the shorter growing season of the xeric and warmer south slope environment. The soil mantle on the north slope is clearly not the Ringold strata but is of aeolian origin. Prevailing winds (southwest) would favor deposition on north-facing slopes and scour the south-facing slopes. The denser north slope vegetation cover also reduces wind speed so that dust is deposited and retained on the north slopes. In essence, this is a positive feedback system: a more mesic environment leads to more vegetation, which leads to more dust buildup, which in turn leads to greater soil depth and water holding capacity and a denser vegetation, and so on.

Presently, most of the vegetative cover on south slopes is provided by the alien annual grass, *B. tectorum*, which suggests that south slopes may have been nearly devoid of herbaceous vegetative cover before the importation of *B. tectorum*. The data gathered in this investigation show that steepness alone does not cause slope barrenness. The data suggest that the interactions between vegetation and microclimate lead to a more favorable environment with more plant cover on the north slopes favoring the deposition of fine-texured soil material to increase soil thickness further.

Generally the slopes are steep and small enough to discourage much grazing use by livestock. Grazing use of the bluffs has been minimal during the past 16 years as observed by the authors, and it is likely that little grazing has been conducted on the bluffs for the past 30 years.

It is possible that valuable mineral deposits that may be surface mined in the future are located beneath steep slopes. Revegetation of steep slopes in dry regions will require an assessment of the original vegetative conditions. It may be necessary and prudent to accept a nearly barren steep slope as revegetated if the exposure is southerly. This point is especially important if land restoration criteria insist upon a return to original conditions.

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Obtaining a Composite Volume-Age Function with the Gompertz Model[2]

Abstract

A procedure for obtaining a single volume-age function for varying site and stand conditions and species is presented. This composite function involves the fitting of the Gompertz model and its coefficients as functions of stand density (average basal area measure), site index (height of dominant and codominants), and quantified species. This procedure is illustrated with data for five interior British Columbia species groups.

Comparison of the ages at which the maximum net mean annual increments calculated from the composite function and from individual models occur indicate they are not different.

Introduction

Volume is one of the most important indices of productivity and is used in the formulation of forest management policies and in the assessment of silvicultural treatments. Volume-age relationships are known to follow the sigmoid shape, and their existence in the form of yield tables dates back to the eighteenth century (Spurr, 1952).

Quite commonly, several volume-age or other convenient relationships are expressed for different species under various site conditions. We present in this paper a procedure for developing a model common to all species for a range of site and stand density classes that is a composite-function.

Important attributes of any volume-age function which have to be considered include the maximum current annual increment (mcai), the maximum mean annual increment (mmai) and the ultimate limiting value. The mmai represents the point of intersection of the cai and mai curves, and is also the point of tangency of the sigmoid curve (yield curve) with the straight line through the origin. The age of the mmai coincides with the physical rotation, that is, the rotation yielding the largest volume of wood per unit area over the length of the period. This coincidence does not necessarily imply the maximum return on the investment. The mcai corresponds to the point of inflection on the yield curve.

The procedure to be described relies heavily on the individual's ability to describe certain conditions accurately. It would be advantageous if coefficients of the model had meaningful biological interpretations, but since the method is only that of mathematical

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description, this requirement is not very essential. It is necessary to have the same model for all the different conditions.

The modified Gompertz function (Winsor, 1932; Grosenbaugh, 1965) is used to demonstrate the method in view of its ability to describe existing British Columbia Forest Service (B.C.F.S.) data accurately (Nokoe, 1974).

The Method

Four main stages (a - d) are recognized.

a) The modified Gompertz function,

$$V = a\, e^{-e^{-c(x-g)}}$$

is fitted to each species group data for every combination of site class and stand density. In this non-linear function, a is the ultimate limiting value, c is a coefficient specifying curve shape, and g is the point of inflection in years. V is net volume in cubic meters per ha (close utilization standard), and x is the age class average in years.

b) The coefficients estimated in the preceding stage are then expressed as functions of species, site index, and stand density, using either linear or non-linear least squares procedure. Site index is the average height of the dominant or codominant trees of a particular species group in a given locality at an index age. This stage involves the quantification of the species.

c) This stage is optional. It involves defining "common" site index and stand density values for all the species under consideration. Such constant values could lead to poorer yield estimates than if the actual values for each species group were used.

d) The composite function could then be reproduced as yield tables or graphs for each species group under the indicated common or actual site indices and stand densities.

Illustration

The objective of this illustration is to obtain a composite volume-age function by site index (SI), and stand density (SD) for five interior B.C. species groups (S), viz. Lodgepole pine (*Pinus contorta* Dougl.), Spruce (*Picea sitchensis* (Bong.) Carr), Aspen (*Populus tremuloides* Michx.) Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), Balsam (*Abies balsamea* (L.) Mill.).

Fourteen sets of species group data with net volume per unit area (m^3/ha), basal area per ha, age, and site indices (and classes), and grouped under five SD classes were available from the basic study by Smith (1973). The SD classes were 1-50, 51-80, 81-120, 121-150, 151+ percent of average basal area per hectare of trees 18 cm diameter at breast height (dbh) and larger. Each SD value may be obtained by any of the following procedures;

(i) using the mid-points of the respective SD classes

(ii) $$SD_{ijs} = \frac{\sum_{k=1}^{a} BA_{ijks}}{\sum_{k=1}^{a} BA_{\cdot jks}} \times 100 \text{ percent}$$

$$SD_{ijs} = \frac{\sum_{k=1}^{a} BA_{ijks}}{\frac{1}{n}\sum_{k=1}^{a}\sum_{i=1}^{n} BA_{ijks}} \times 100 \text{ percent}$$

or (iii) $$SD_{ijs} = \frac{1}{a}\sum_{k=1}^{a} \frac{BA_{ijks}}{\overline{BA}_{.jks}} \times 100 \text{ percent}$$

for $i = 1, \ldots, n$ (n SD classes = 5 in our case)
$j = 1, \ldots, m$ (m Site classes = 3 " " ")
$k = 1, \ldots, a$ (a Age classes = 12 " " ")
$S = 1, \ldots, 1$ (1 Species groups = 5 " " ")

where BA is basal area, and SD_{ijs} is the average stand density for species S, Site class j and SD class i for all ages. The notation $BA_{.jks}$ is the average basal area for species S, site class j and age class k; that is,

$$\overline{BA}_{.jks} = \frac{n}{1}\sum_{i=1}^{n} BA_{ijks}$$

Procedure (i) is not appropriate for stand classes with unequal widths, and (ii) is based on a linear relationship of average basal area with age which is untrue. Procedure (iii) was used in this study because of the limitations of (i) and (ii).

Stage 1: Estimates of the Gompertz coefficients a, c, g, (available on request) were obtained for each set of data using the UBC-BMDX85 non-linear computer program. This program, which is an adaptation from the BMDX85 program of the UCLA Documentation Center, uses the modified Gauss-Newton iterative procedure described by Hartley (1961).

Stage 2: The five species were quantified as follows:

1—lodgepole pine, 2—spruce, 3—aspen, 4—Douglas fir, and 5—balsam. Thus the variable S took on values of 1 to 5, whole numbers only. Coefficient estimates a, c, g were then expressed as functions of S, SD, SI and their transformations using the linear regression program developed by A. Kozak, with the condition that each of the independent variables S, SD, and SI occurred at least once in any of the three functions. The results obtained from this example were of the following form:

eqn 1: $a = f(S^3, S^4, SD^2, SD^3, SD^4, SI_1 * SD)$; $R^2 = .9006$ $SE_E = 60.0 m^3/ha$

eqn 2: $c = F(S, S^2, S^3, S^4, SI, SD^2, SD^3, SD^4, SD * SI, SD^2 * SI)$; $R^2 = .4996$ $SE_E = 0.0089$

eqn 3: $g = f(S, S^2, S^4, SI, SI^2, SD)$; $R^2 = .7585$ $SE_E = 8.6$ years

These regressions were highly significant with fairly high coefficients of multiple determination; $R^2.SE_E$ represents the standard error of the estimate of the dependent variable. The values of *a* from the various conditions used in obtaining the above functions

ranged from 43.3 to 746.6, c ranged from 0.013304 to 0.074360, and g was from 21.765 to 114.42. Thus the SE_E obtained from the functions of a, c, g could be regarded as fairly reasonable.

Stage 3: To compute final yields from the composite model, "common" values for site index and stand density were used. Instead of using these values, use could have been made of the separate species values as indicated in Tables 1 and 2. These tables were derived from the basic data of Smith (1973).

TABLE 1. Height of dominants and codominants in meters at age 100 (Site indices) for interior British Columbia species groups.

Species group		Site indices		
Code	Name	Site 1	Site 2	Site 3
1	Lodgepole pine	27.1	22.3	16.8
2	Spruce	29.6	23.5	16.8
3	Aspen	—	27.4	19.5
4	Douglas fir	30.5	22.9	19.5
5	Balsam	29.0	22.6	17.7
	Average	29.0	23.7	18.1
	"Common"	29	24	18

The large differences in the average SD values for SD class 151+ were due to the open nature of the class. Accordingly, two "common" values of 170 and 205 were allocated to the class.

Stage 4: Final yield tables were then computed for species 1—5, SD 30—205, for site indices 29.0, 24.0, and 18.0 using the modified Gompertz model,

Table 2. Stand density values in percentages.

SD class		1-50			51-80			81-120			121-150			151+		
Species	SC	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
1	Lodgepole pine	38	33	30	68	67	66	100	102	96	132	134	136	180	193	225
2	Spruce	37	32	28	69	67	64	103	100	102	134	133	131	178	177	210
3	Aspen	—	33	29	—	67	69	—	102	95	—	133	144	—	175	208
4	Douglas fir	37	35	35	69	66	67	99	100	100	134	136	135	167	204	208
5	Balsam	40	34	33	64	69	66	97	99	98	131	135	139	185	175	203
Average		38	33	31	68	67	66	100	101	98	133	134	137	178	185	210
"Common"			30			65			100			135			170	205

$$V = (\text{eqn.1})\, e^{-(\text{eqn2})\,(x\,-\,\text{eqn.3})}$$

Maximum mai values for each species were then computed using the common site index respective species site index value. Table 3 provides summaries of the results for lodgepole pine (SC 1, 2, 3) and aspen (SC 2, 3). The predicted volumes (V) varied for the two approaches (common versus species site index), but the ages (A) at which these maximum values were attained were similar.

Conclusion

A method of obtaining a composite volume-age function has been presented. This method is simple and requires a minimum amount of time and computation. It is not

TABLE 3. Part summary of variable density estimates of yields*, mean annual increment (mai), and ages at which mais are maximum by site and SD classes.

Species group	**	SD 30 A	V	mai	65 A	V	mai	100 A	V	mai	135 A	V	mai	170 A	V	mai	205 A	V	mai
Lodgepole pine	1c	85	141	1.66	90	226	2.51	87	314	3.61	85	346	4.66	75	437	5.83	75	529	7.05
"	" 1	90	121	1.34	90	202	2.24	86	296	3.44	90	408	4.53	90	516	5.73	—	—	—
"	" 2c	110	146	1.33	100	194	1.94	100	276	2.76	95	348	3.66	83	368	4.43	80	404	5.05
"	" 2	110	93	0.84	106	151	1.42	103	221	2.15	96	286	2.98	108	407	3.77	—	—	—
"	" 3c	115	91	0.79	120	137	1.41	120	198	1.65	113	245	2.17	110	271	2.46	110	278	2.52
"	" 3	126	50	0.39	122	89	0.73	115	121	1.05	118	175	1.48	100	206	2.06	—	—	—
Aspen	2c	125	69	0.55	115	122	1.06	113	199	1.76	108	286	2.65	105	349	3.32	98	378	3.86
"	2	126	146	1.16	112	181	1.61	114	302	2.65	104	341	3.28	104	408	3.92	—	—	—
"	3c	116	22	0.19	120	59	0.49	126	115	0.91	120	169	1.41	117	202	1.73	118	209	1.77
"	3	109	28	0.26	126	101	0.80	128	136	1.06	92	151	1.64	114	242	2.12	—	—	—

** c—composite site index value used. e,g. 1c etc; otherwise from specific data.

* A is age in years; V is **cubic meter per hectare to a close utilization standard,** net for decay only; mai is the yield divided by the age at which annual growth culminates to the nearest tenth.

restricted to the Gompertz function. The only requirement is that the same model should be used in describing each species and/or site conditions. Such models should be able to fit the data adequately. The method may also be applied to a single species; in this case, "species" will no longer be a variable.

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Rationale of the Distribution of the Sculpin, Cottus sp., in the Salmon River, Idaho

Abstract

The distribution of the sculpin, *Cottus* sp., in certain areas of the Salmon River which are critical for the spawning and nursery of the Chinook salmon was studied for suggestions of the explanation of the distribution. The inhabitation of two tributaries and the non-inhabitation of the headwaters of two other tributaries can best be explained by the available data as demonstrating a prey preference for the Chinook salmon over the Dolly Varden and the Eastern Brook char. The number of individuals of the sculpin family present, the average size of the individuals, and the mouth gape of a random specimen emphasize a potential predator problem.

Introduction

Control of the predation and competition of the sculpin, *Cottus* sp., in certain sections of the Salmon River of Idaho seems to be indicated (Primbs and Platts, 1976). Since such control would be facilitated by determining the distribution of the sculpin in this drainage, sampling of the total fish population within five representative areas of the Salmon River during July, August, and September of 1976 was made, and the pattern of the distribution within these areas was studied for suggestions of the explanation of the distribution.

Methods

During summer low stream flow, total fish populations were sampled at five sites on four tributaries of the Salmon River—the South Fork of the Salmon River, Johnson Creek, Bear Valley Creek, and Frenchman Creek: one site was located on each tributary, except on Bear Valley Creek, which was sampled at two sites approximately two miles apart (Fig. 1).

The sampling sites extended approximately 549 m. Collections were made twice over the entire 549 m in 3-m sections at a time by setting a seine at the downstream terminus of the section sampled and by then operating a Smith-Root electrofisher first in an upstream direction and then in a downstream direction. Fish were collected continuously after stunning by use of two hand nets and finally by inspection of the seine when the 3-m section was completed. The genus or the species (primarily in one case of the game fish), the total length, and the individual body mass were determined for all fish collected.

Results and Discussion

In the headwaters of two tributaries—Johnson Creek and the South Fork of the Salmon River—no sculpins were found. A partial explanation of the absence of sculpins in Johnson Creek may be the Deadhorse Rapids, which could at low water serve as a

barrier to the movement of sculpins (Corley, pers. comm., June 1977). In Johnson Creek the Eastern Brook char (*Salvelinus fontinalis*) was the preponderant species inhabiting the area, whereas in the South Fork the Dolly Varden char (*Salvelinus malma*) was the exclusive and only species occurring. At the two Bear Valley Creek sites and at the site on Frenchman Creek, however, sculpins were found in large numbers, numbers which have a positive correlation with the numbers of Chinook salmon (*Oncorhynchus tshawytscha*) (Table 1).

Johnson Creek and the South Fork of the Salmon River are both anadromous fish spawning areas (U.S. Fish and Wildlife Service, 1964), and Chinook salmon are numerous in both streams. But the sites sampled were in the headwater reaches of these two

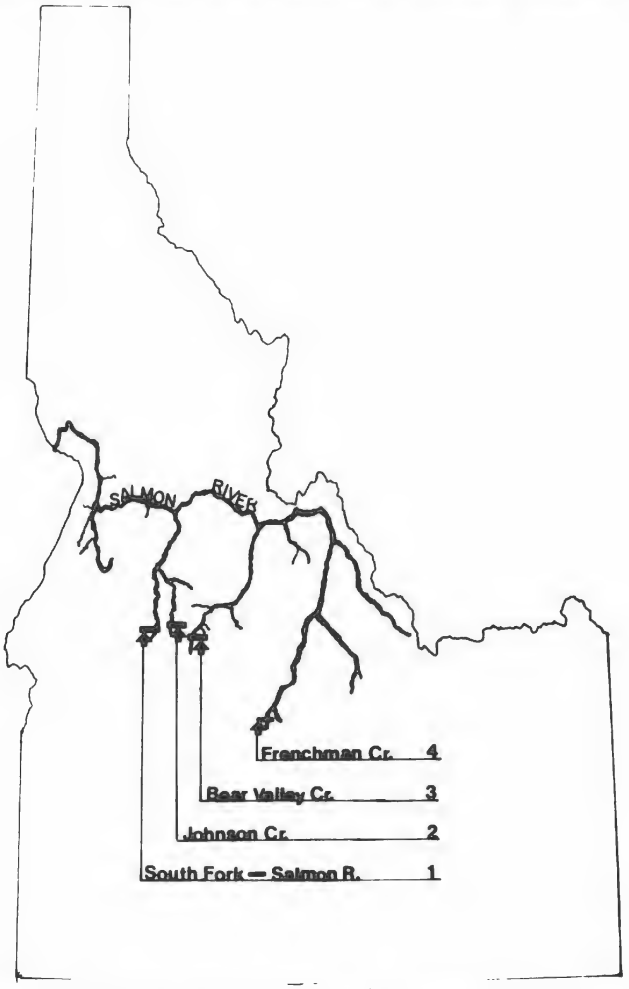

Figure 1. Sampling sites on four tributaries of the Salmon River, Idaho. One site was located at each point marked on map above except on Bear Valley Creek, which was sampled at two sites approximately two miles apart.

streams, beyond the migration range of the Chinook. The sculpin (*Cottus beldingi*) has been reported to be absent from uppermost waters (Gord and Flittner, 1974; Maughan, 1976). Other sculpins, however, do inhabit headwaters—e.g., the Columbia sculpin (*Cottus hubbsi*) (Maughan, 1976). Of the sculpins captured, approximately 2 percent were identified down to species, and the entire 2 percent randomly sampled belonged to the species *Cottus hubbsi*. The sculpins identified down to species were taken from the Big Meadows site of Bear Valley Creek in 1976 and from the Stolle Meadows site of the South Fork of the Salmon River in 1975 (Primbs and Platts, 1976). The Stolle Meadows site is 9.7 km downstream from the headwaters site sampled in 1976 and reported herein. At the Stolle Meadows site Steelhead trout—Rainbow trout (*Salmo gairdneri*) were also found in 1975.

TABLE 1. Number of sculpins and other fish collected within 549 meters of stream length.

Stream	Sculpins	Chinook Salmon	Rainbow Trout	Eastern Brook Char	Dolly Varden Char	Mountain Whitefish	Squawfish
Bear Valley Cr. (Big Meadows)	649	61	9	24	11	2	0
Bear Valley Cr. (Mace Meadows)	1179	122	81	56	19	11	0
Frenchman Cr.	1515	575	0	510	0	29	0
Johnson Cr.	0	0	2	233	0	0	1
South Fork-Salmon River	0	0	0	0	141	0	0

It has been shown under aquaria conditions that the Torrent sculpin has a prey preference among the various species of salmon; the preference was least for the Chinook and Coho salmon (Patten, 1975). It appears from the data presented above and the results of other studies cited herein that, in addition to an environmental requirement equivalent to the Chinook's, the sculpin (*Cottus hubbsi* and/or other species) successfully inhabiting certain areas of the Salmon River have also a prey preference for the Chinook over the Dolly Varden or Eastern Brook trout.

The tendency of sculpins to prey on salmon increases with the body size of the sculpin (Patten, 1971). The critical length for the Slimy sculpin (*Cottus cognatus*) at or above which the sculpin will prey on trout eggs and fry is 5.0 cm (Clary, 1972; Northcote, 1954). The percentages of sculpins exceeding 5 cm in the three tributaries sampled ranged from 74 to 86 percent, statistics which emphasize the predator potential of the sculpins in the Salmon River (Table 2). Two of the captured Columbia sculpin had a total length of 81 mm; the mean measurement of their mouth gape was 9.5 mm, a factor which again emphasizes the predator potential.

TABLE 2. Statistics on total length of sculpins collected.

Stream	Mean Length (cm)	Extremes Min. (cm)	Extremes Max. (cm)	Percentage of Sculpins Exceeding 5 cm
Bear Valley Cr. (Big Meadows)	6.2	1	10	81
Bear Valley Cr. (Mace Meadows)	5.9	2	11	74
Frenchman Cr.	7.0	1	11	86

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Some Nitrogen Fractions in Two Forest Soils and Their Changes in Response to Urea Fertilization

Abstract

Some soil N fractions were determined for two low-site Douglas-fir forest soils, the Everett and Alderwood Series. Ammonium and nitrate levels were low for both soils, so turnover must be at least ten times per year in order to meet stand uptake requirements. Urea fertilization increased soil ammonium levels by 100 fold within three days, but levels dropped to near those of the control after 220 days. Soil nitrate levels remained low throughout this period. After 220 days, most fertilizer N was accounted for in the residual (or humin plus fixed N) fraction of the Alderwood soil. Variability was so great for the Everett soil that fertilizer N could not be accounted for. Data from previously fertilized plots suggest a seasonal elevation in soil ammonium levels (by two-to three fold) for at least five years after fertilization.

Introduction

It has been known for over two decades that nitrogen is potentially limiting in soils of the Douglas-fir region, and growth response to N fertilization has been demonstrated in many cases (Gessel and Walker, 1956; Gessel *et al.*, 1969). However, amounts of added N necessary for growth response are typically small relative to total soil N levels (Heilman and Gessel, 1963). Clearly, response is due to changes in the levels of available soil N, yet little has been done on available soil N levels in this region. The purpose of this study was to determine available soil N levels in two low-site Douglas-fir forest soils, and to observe changes in soil N fractions brought about by urea fertilization.

In his urea fertilizer studies, Crane (1972) demonstrated the presence of urease (a common soil enzyme involved in the hydrolysis of urea) in the Everett soil at the site where this study was conducted. In laboratory studies using humus from a black spruce stand, Roberge and Knowles (1966) found nearly all applied urea-N could be accounted for as NH_4^+ within three days, suggesting that ureolysis (urea hydrolysis) is rapid. Crane (1972) takes issue with this estimate, concluding from his detailed studies on temperature and mixing effects that complete hydrolysis requires 10 to 20 days in undisturbed coniferous forest soils.

Crane (1972) and Overrein (1972) found little nitrate leaching following urea fertilization of coniferous forest soils in Washington and Norway, respectively. Roberge and Knowles (1966) found little nitrate production in their lab studies of urea-amended soils. In similar laboratory incubation studies, Heilman (1974) found nitrate production in soils from the Pacific Northwest to vary considerably, being most closely correlated with soil total N and C levels. Urea treatment of these soils caused increased nitrate production, but results varied widely. Of the 18 soils tested, the Everett series produced the least nitrate under all treatments.

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Based on the above studies and the observation that the Everett and Alderwood soils are low in total N, it was hypothesized that soil NH_4^+ and NO_3^- levels would be low in each soil, and that urea fertilization would result in a large increase in soil NH_4^+ levels within 20 days. The net immobilization rate of NH_4^+ (uptake by soil organisms minus mineralization) was unknown, but tree growth response typically lasts three to five years (Gessel *et al.*, 1969), which suggests that soil NH_4^+ levels should remain elevated for at least three years. On the basis of Crane's (1972) data for this site, as well as other literature for forest soils (Heilman, 1974; Overrein, 1971; Roberge and Knowles, 1966), it was expected that soil NO_3^- levels would increase only slightly, if at all, after fertilization.

Sites

The study was conducted at the A. E. Thompson site in the foothills of the Washington Cascades about 45 mi southeast of Seattle. Mean annual precipitation at the site is 186 cm, mosly in the form of rain. A two to three month summer drought is common. Mean January and July temperatures are 2.8 and 16.8°C, respectively.

The study sites were located in 47-year-old, site IV Douglas-fir (*Pseudotsuga menziesii*) stands. Understory at both sites consists primarily of salal (*Gualtheria shallon*) and Oregon grape (*Berberis nervosa*), with occasional vine maple (*Acer circinatum*). Oregon grape was more abundant on the Alderwood than on the Everett site.

The Everett soil is derived from coarse glacial outwash and consists of more than 60 percent gravel, less than 5 percent silt plus clay, and low base saturation (Cole and Gessel, 1968). It is classified as a Dystric Xerochrept (USDA-SCS, 1973). The soil is excessively drained and droughty during summer months.

The Alderwood soil is derived from gravelly ablation till of low base saturation overlying an impermeable basal till at a depth of 60-80 cm. It is moderately well drained except in flat areas or depressions. It is classified as an Entic Durochrept (USDA-SCS, 1973). See Cole and Gessel (1968) for detailed descriptions of the two soils.

Methods

On each soil type, 3 x 3 m plots were fertilized with 200 kg/ha urea-N in February, 1976. Control areas were designated nearby. The fertilized plots were sampled three days after fertilization and at weekly intervals thereafter for five weeks. They were then sampled monthly for the duration of the study. The control plots were sampled at monthly intervals throughout the study.

At each sampling, five random cores 4 cm in diameter were taken from the top 15 cm of soil. At 60, 180, and 220 days after fertilization the 15-30 cm soil layer was sampled as well. The upper 15 cm of soil was concentrated upon because Crane (1972) found negligible N leaching past this depth following urea fertilization at the site. Soil cores were kept moist and refrigerated at 4°C after collection until being extracted (within 24 hours) for NH_4^+ and NO_3^-. After shaking 20 g wet soil with 100 ml of 1N KCl for four hours, supernatant solutions were analyzed for NH_4^+ and NO_3^- using a Technicon Autoanalyzer II. Soil moisture was determined by oven drying a subsample of soil at the time of KCl extraction.

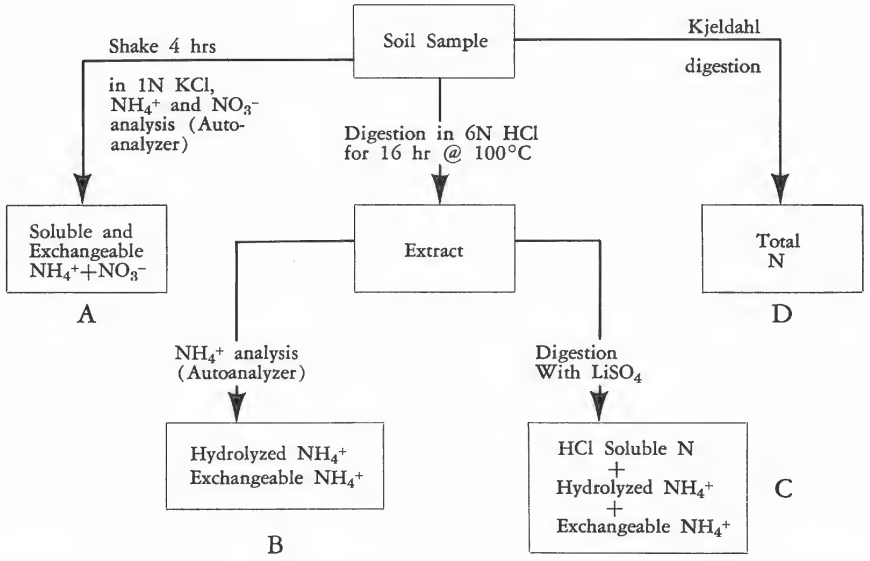
In an attempt to recover immobilized fertilizer N, soils were analyzed for total N and for selected N fractions after fertilized plot NH_4^+ levels had dropped to near those

of the control plots (day 220). The N fractionation scheme is shown in Figure 1; it is a simplified version of the method given by Cheng and Kurtz (1963) and adapted by Jorgensen (1967) to forest soils. The major difference between this scheme and that of Cheng and Kurtz is that no attempt was made to account for various humin and fixed N fractions. Efforts were concentrated instead on the more "available" forms of soil nitrogen.

Results

Soil NH_4^+ values in the control plots showed considerable variability but ranged between one and four ppm (Fig. 2). Some seasonal variation was evident. Except for a mid-summer depression and a peak in October, soil NH_4^+ levels were tied closely with changes in monthly temperature (Fig. 3).

Nitrogen Fractionation Scheme



Fraction	Source	Analogous Fractions from Cheng and Kurtz
Exchangeable NH_4^+	A	Exchangeable NH_4^+
Soluble NO_3^-	A	Soluble NO_3^-
HCl hydrolyzed NH_4^+	B-A	Hydrolyzed NH_4^+
HCl soluble N	C-B-A	Amino sugar + Amino Acid N*
Residual N	D-C-B-A	Acid-soluble humin N + Fixed NH_4^+ + insoluble humin N
Total N	D	

*Cheng and Kurtz separated these by making the HCl extract alkaline and distilling to obtain amino sugar N, whereas in this study no alkalization was carried out.

Figure 1. Flow chart for soil nitrogen fractionation.

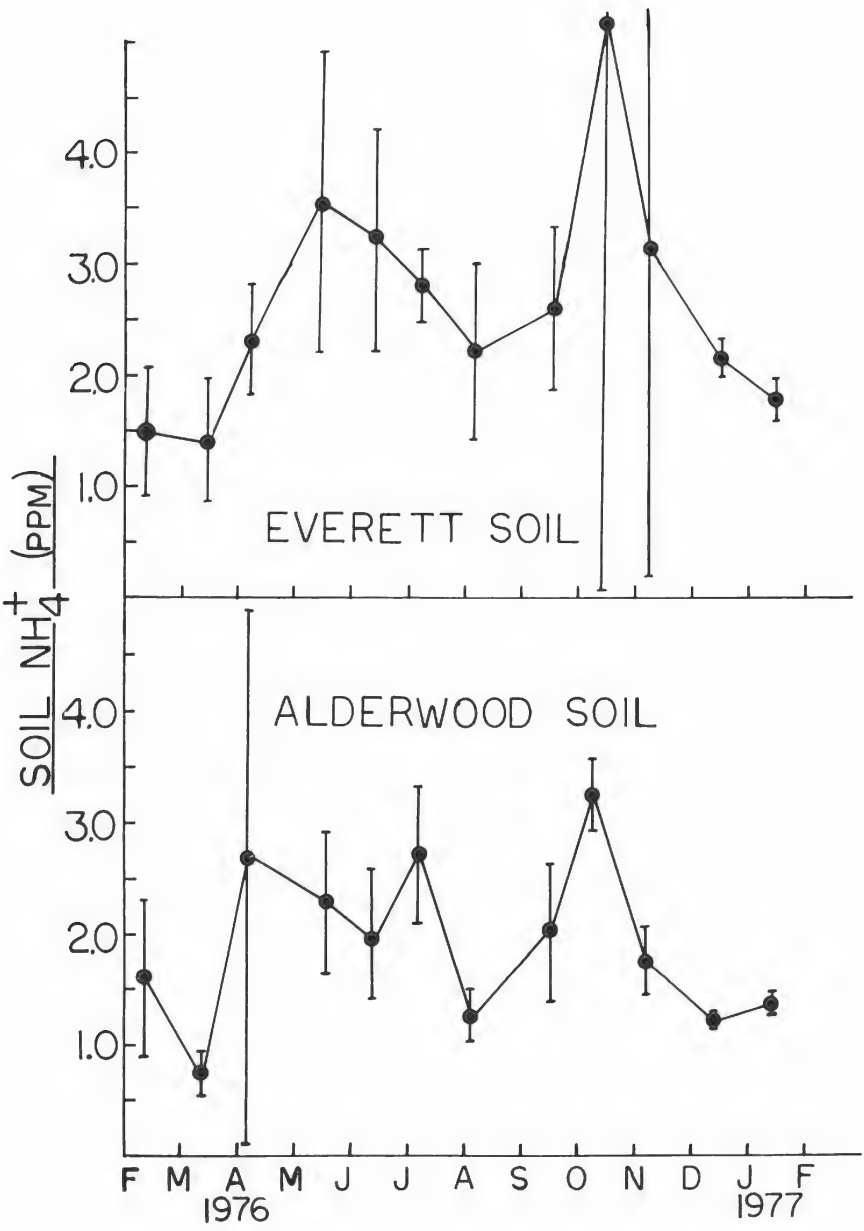


Figure 2. Seasonal variations in soil NH_4^+ levels (0-15 cm depth). Standard errors are shown.

Soil NO_3^- values were variable but quite low, at no time exceeding 0.3 ppm. Unlike soil NH_4^+ levels, there was no increase in soil NO_3^- during the spring, but there *was* an increase during the fall and winter months. Since NO_3^- leaches easily from the soil, a buildup of NO_3^- might occur if nitrification occurs during periods of low precipitation. Precipitation was lower than normal in the fall and winter of 1976-77, but not lower than during the preceding summer (which was unusually wet). Thus, it seems unlikely that the soil NO_3^- buildup in fall and winter is due to low precipitation alone.

Urea fertilization increased soil NH_4^+ levels by 100 fold within three days for both soils (Fig. 4). After 30-60 days, NH_4^+ levels began dropping, and by 220 days there was no statistically significant difference ($\alpha < .05$) between control and fertilized NH_4^+ levels.

Soil NO_3^- increased more slowly than NH_4^+ after fertilization, reaching peak values at 150-180 days. Soil NO_3^- values were extremely variable during this peak period,

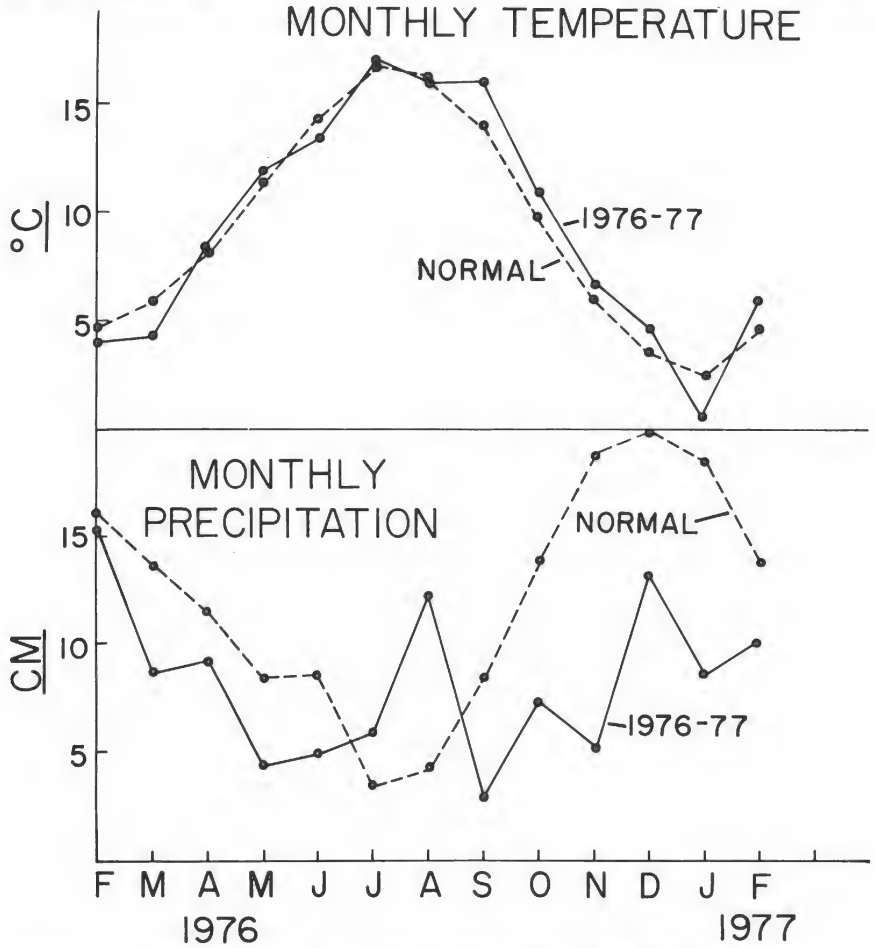


Figure 3. Monthly temperatures and precipitation from the Landsberg, Washington, weather station.

with occasional values that were 10-100 times higher than the mean. Excluding the extreme values, mean NO_3^- never exceeded 0.6 ppm for the Everett soil or 1.2 ppm for the Alderwood soil. Four of the extreme values (less than 3 percent of the entire sample population) ranged between 4 and 12 ppm, and a fifth yielded a value of 48 ppm.

That the variation among nitrate values is due to horizontal spatial variation in the field is evident from the data of Table 1. Control soil NO_3^- values were low and fairly consistent from point to point, but NO_3^- levels in the fertilized plots showed high hori-

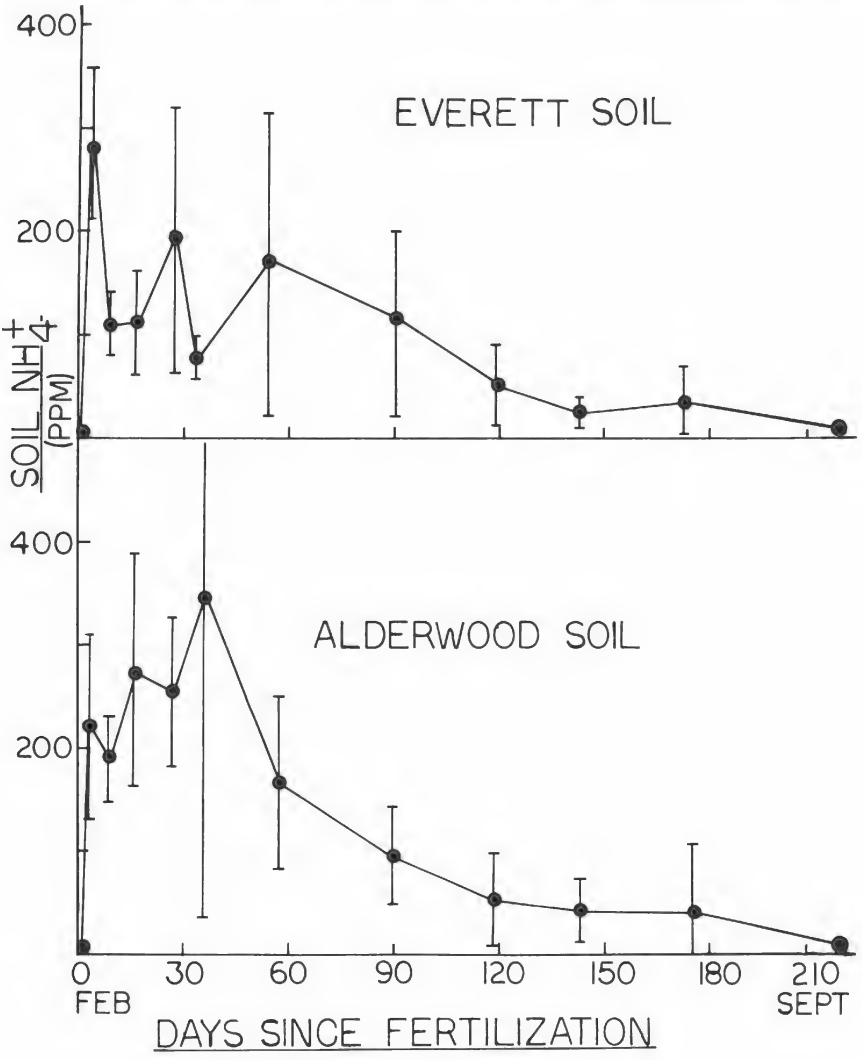


Figure 4. Soil NH_4^+ levels after fertilization with 200 kg/ha urea-N. Standard errors are shown.

zontal spatial variation, with the value for the top (0-15 cm) section of each core being highly correlated (r^2=0.99) with the value for the bottom (15-20 cm) section of the same core. Such variation probably arises from variations in fertilizer distribution, water movement patterns, and microorganism populations in the field.

Fractionation of soil N showed that the untreated Everett soil has a significantly (α=0.05) higher total N level than the untreated Alderwood soil, although the latter had a greater amount of HCl hydrolyzed NH_4^+ plus HCl soluble N (Table 2). Residual and total N levels for the fertilized Alderwood soil were statistically (α=0.05) greater than residual and total N levels for the untreated Alderwood soil, implying that most fertilizer N had been incorporated into the humin and fixed N fractions by this date. Mean values for total N of the fertilized Everett soil were almost identical to those of the control plots, and the variability was quite high, so no statistically valid conclusions about changes could be drawn.

It was possible to examine some longer-term effects of fertilization on the Everett soil by sampling plots previously fertilized by Turner (1975) and as part of the

TABLE 1. Soil NO_3^- levels at two depths for replicate cores of the Everett and Alderwood soils 173 days after urea fertilization (ppm in soil, based on the <2 mm fraction).

Core Number	1	2	3	4	5	1	2	3	4	5
	Everett, Control					Alderwood, Control				
0-15 cm	0.05	0.07	0.07	0.07	0.05	0.06	0.06	0.07	0.05	0.05
15-30 cm	0.07	0.08	0.04	0.59	0.05	0.05	0.05	0.07	0.06	0.06
	Everett, Fertilized					Alderwood, Fertilized				
0-15 cm	47.98	1.50	0.97	0.04	0.02	2.69	0.09	0.08	12.45	0.13
15-30 cm	33.61	1.32	1.95	0.07	0.07	3.59	0.60	0.05	11.51	0.34

TABLE 2. Nitrogen fractions in control and fertilized soils 220 days after fertilization, including standard deviations and percent of total N present (in parenthesis).

	NO_3^-	NH_4^+	HCl Hydrolyzed NH_4^+	HCl solution N	Residual N	Total N
			Everett, Control			
0-15 cm	0.2±0.1	2.4±0.8	312±10**	547±131	908±100	1770±130**
	(0.01%)	(0.1%)	(18%)	(31%)	(51%)	(100%)
15-30 cm	0.2±0.1	2.2±0.6	394±44	463±82	611±54	1470±50
	(0.01%)	(0.1%)	(27%)	(31%)	(42%)	(100%)
			Everett. Fertilized			
0-15 cm	0.2±0.1	4.5±2.0	323±0**	583±207	890±174	1800±210
	(0.01%)	(0.3%)	(18%)	(32%)	(49%)	(100%)
15-30 cm	0.3±0.3	4.5±3.3	355±33	408±129	713±87	1450±90
	(0.02%)	(0.3%)	(24%)	(28%)	(48%)	(100%)
			Alderwood, Control			
0-15 cm	0.1±0.02	1.8±0.6	365±27**	592±59	471±35	1430±10**
	(0.01%)	(0.1%)	(26%)	(41%)	(33%)	(100%)
15-30 cm	0.1±0.03	1.2±0.3	326±24	570±29	493±17	1390±10
	(0.01%)	(0.1%)	(23%)	(41%)	(35%)	(100%)
			Alderwood, Fertilized			
0-15 cm	0.3±0.4	7.1±5.7	399±16**	649±18	684±30*	1740±50*
	(0.01%)	(0.4%)	(23%)	(37%)	(39%)	(100%)
15-30 cm	0.2±0.2	3.2±1.5	321±12	514±35	712±96*	1550±210
	(0.01%)	(0.2%)	(21%)	(33%)	(46%)	(100%)

*Difference between this and control soil is significant at the 95% level, t-test.
**Difference between Alderwood and Everett soil is significant at the 95% level, t-test.

Regional Forest Nutrition Research Project (RFNRP; Gessel *et al.*, 1969). Applications of 220 kg/ha urea-N had been made in both cases. Soil NO_3^- levels were consistently below 0.1 ppm in all cases and showed no apparent differences with fertilization. A final sample taken in February, 1977 (12 months after fertilization) during the present study indicated little difference between control (1.02 ppm) and fertilized (1.35 ppm) soil NH_4^+ levels. Likewise, samples taken in January 1976, 23 months after fertilization of Turner's plots, showed virtually no difference in NH_4^+ levels (1.34 vs 1.37 ppm). In July of 1976, however, soil NH_4^+ levels in Turner's fertilized plots had increased by over 100 percent above control levels (4.09 vs 1.69 ppm), and a similar situation occurred for the RFNRP plots in April 1976, 6½ years after fertilization (1.93 vs 0.96 ppm). The data are limited at present, but suggest that fertilization can result in increased soil NH_4^+ levels during the spring and summer months for at *least* a five year period. Further sampling on a seasonal basis will be needed to verify this conclusion, however.

Discussion

Soil NH_4^+ in the untreated sites constitutes only about 0.1 percent and NO_3^- constitutes less than 0.01 percent of the total soil N present in either soil. This finding represents about 3-6 kg/ha of NH_4^+ and 0-3.6 kg/ha of NO_3^- for these soils. Turner (1975) estimates annual N uptake in these forest stands at approximately 40 kg/$ha^{-1}yr^{-1}$, so it is clear that the NH_4^+ plus NO_3^- pools in these soils must turn over at least 10 times per year to meet stand requirements, exclusive of soil microbiological needs. Fluxes into and out of the soil NH_4^+ and NO_3^- pools must be large relative to pool size, so one would expect seasonal changes in uptake, mineralization, or other processes.

The seasonal changes in soil NH_4^+ reported here are similar to those reported by Ellis (1974) for mineral N ($NH_4^+ + NO_3^-$) and N mineralization rates in a maple woodlot and an old field soil in Ontario: a spring increase, a mid-summer decrease, a fall peak, and winter decrease. He found that short-term changes in soil temperature and moisture had little apparent effect on the direction of such seasonal changes, and felt that the observed patterns were a response to phenological changes of the vegetation. On the other hand, he noted seasonal changes in C mineralization which were closely correlated with soil temperature trends.

In this study, NH_4^+ mineralization apparently exceeded uptake and nitrification in the spring and fall, whereas the trend appeared to be reversed in the summer and winter. Changes in soil NH_4^+ levels coincided somewhat with monthly temperatures, except for the summer depression in soil NH_4^+ levels. In a normal year, moisture limitations on N mineralization might be used to explain the summer depression, but it is doubtful that moisture was limiting in the wet 1976 summer. A phenological explanation appears more appropriate. Since NO_3^- is easily leached and can be denitrified, it is difficult to interpret variations in soil NO_3^- levels. It is clear, however, that nitrification exceeded uptake, leaching, and denitrification in the fall, when soil NO_3^- levels increased.

As expected, soil NH_4^+ levels increased dramatically after fertilization. Contrary to Crane's (1972) predictions, however, ureolysis seemed to be nearly complete or complete within three days. Mean values indicate that NH_4^+ levels began decreasing earlier

and more rapidly in the Everett than in the Alderwood soil, but the variations were too great to permit definitive statements about the differences. Mean soil NO_3^- levels remained low relative to NH_4^+ at all times, but increased between days 90 and 180, implying that nitrification rates exceeded uptake, leaching, and denitrification rates during this period. It is impossible from the data to know which of the processes changed.

After soil NH_4^+ had returned to the control levels, nearly all of the fertilizer N (approximately 180 kg/ha out of 200 applied) could be accounted for by increases in Alderwood total soil N values, with most of the increase occurring in the residual (or humin plus fixed NH_4^+) fraction. Results from the Everett soil were inconclusive, due to the high variability. On the same soil at this site, Crane (1972) found little volatilization or leaching following urea fertilization, and Turner (1975) estimated aboveground tree uptake to be only 35 $kg/ha^{-1}yr^{1}1$ following a 200 kg/ha urea fertilization on the same soil at the same time of year at this site. Hence, it seems likely that most fertilizer N was immobilized in the Everett soil, as it was in the Alderwood soil, with differences being masked by plot-to-plot and sampling variations.

These results contrast to those of Cheng and Kurtz (1963) and Stewart *et al.* (1963) for agricultural soils, and to those of Chu and Knowles (1966) for a black spruce forest soil, where most of the fertilizer N was found in the soluble alkali (amino acid) soil N fraction. This fraction should theoretically be included in the HCl-soluble fraction here (Fig. 1). Baker (1973), on the other hand, found that N fertilization caused a decrease in the amino acid soil N fraction, with most fertilizer N being accounted for in the exchangeable NH_4^+ and NO_3^- forms.

The length of time since fertilization is probably an important factor in explaining such differing results. Had samples been taken at day 90 in this study (which is about the time that Baker sampled), about half of the fertilizer N would still have been accounted for as NH_4^+ (Fig. 4). As discussed by Chu and Knowles (1966), soil N is undoubtedly dynamic in nature, so a buildup in the humin N fraction would be expected as by-products of microbial cell turnover accumulate.

The data from plots fertilized previous to this study suggest a seasonal re-release of additional NH_4^+ (above levels in unfertilized plots) for at least five years. Whether this release emanates from some soil N fraction or from N-enriched litter is unknown, however. Some fertilizer N is stored in older foliage (Turner, 1975) and this fact undoubtedly contributes to the prolonged growth responses observed (Gessel *et al.*, 1969).

Summary and Conclusion

1. Soil NH_4^+ and NO_3^- levels were very low in the untreated, low-site Douglas-fir soils studied. These N fractions must turn over at least ten times per year in order to meet tree uptake demands;

2. Seasonal patterns suggest that there is more NH_4^+ mineralization than uptake during the spring and fall months, and less mineralization than uptake during the winter months;

3. Urea fertilization caused a 100-fold increase in soil NH_4^+ levels within three days, but NH_4^+ levels were down to near those of the untreated soils by 220 days. Soil NO_3^- levels remained low (<1 ppm) throughout the study, but tended to increase between days 90-180, implying that nitrification exceeded NO_3^- uptake, leaching, and denitrification during this period;

4. Most fertilizer N could be accounted for in the residual (humin plus fixed N) fraction of the Alderwood soil, but the fertilizer N could not be accounted for in the Everett soil, due to excessive variability; and

5. It appears that soil NH_4^+ levels may remain somewhat elevated during the spring and summer months for a least five years following urea fertilization on the Everett soil. It is not known whether this elevation is due to remineralization of some soil N fraction or to decomposition of the N-enriched litter.

Clearly, most N in these two soils is in relatively unavailable forms, and most fertilizer N is quickly incorporated into such forms. A small fraction of the fertilizer N may remain in an active form that is remineralized during spring and summer months for years after fertilization, however. If so, the nitrogen fractionation methods adapted from Cheng and Kurtz (1963) are apparently not sensitive enough to characterize this mineralizeable N fraction. Further incubation studies, including some aspects of nitrification, are now being conducted by David Breuer and this author at the College of Forest Resources, University of Washington. Results will be reported in a later paper.

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Tectonic Significance of Regional Jointing in Columbia River Basalt, North-Central Oregon

Abstract

In a substantial portion of the terrain covered by Columbia River Basalt in northern Oregon, angular drainage patterns with numerous linear segments are common instead of dendritic ones. These patterns were examined on LANDSAT, Skylab, and U-2 high flight imagery for two areas. These areas include (1) about 1000 km^2 around Big Summit Prairie and (2) about 3700 km^2 around Condon and Heppner. Rose diagrams were prepared for several subareas in each area and one pattern is found in all cases. It consists of three main directions about 30° apart at Big Summit Prairie and about 40° apart at Heppner. In the Big Summit Prairie area these are known to be joint sets that pass through multiple flows of Columbia River Basalt. They are found to be related to folding. The central set (set A) is perpendicular to the fold axes and the other two (sets B and B′) are symmetrically arranged at about 30° to either side of the first set. Set A is interpreted as tensile joints formed perpendicular to the fold axes and sets B and B′ as conjugate shear joints formed symmetrically to the compression that produced the folding. Similar joints were not previously known in the Heppner area, but the pattern there has the same relation to folding as is found at Big Summit Prairie and the same interpretation is proposed. Minor complications of the patterns include features related to a northwest trending fold in the northeast corner of the Big Summit Prairie area and a N64°-69°E trending linear that crosses the southern portion of the Heppner area. The origin of this last feature is uncertain.

Introduction

Little study has been devoted to regional joint patterns found in the basalts of the Columbia River Group of southeastern Washington and northeastern Oregon. The prevalence of complex patterns of cooling joints in practically all outcrops of the unit has encouraged the impression that no systematic analysis is worthwhile. However, investigators have long been aware of the presence of such joints in one area, namely, around Big Summit Prairie (Fig. 1) in Crook County, Oregon (Oles, pers. comm., 1975). Here, relatively thin flows of Picture Gorge Basalt of the Columbia River group, around 200 m thick (Waters, 1961), rest on top of very weak John Day Formation tuffs in the dip slope of the tilted fault block that forms the Ochoco Mountains. Regional joints have been opened by landsliding of the entire basalt unit down this south trending dip slope (Lawrence, 1974). The pattern is spectacularly displayed on Landsat (formerly ERTS) red band imagery by the dark tone of the pine forests in the valleys carved along the joints and the contrasting light tone of the intervening grass and sage vegetation on basalt highs. Landsat and Skylab imagery show similar but much less distinct angular relations between linear drainage segments on the north dipping flank of the Blue Mountain anticlinorium south of the Columbia River (Heppner area, Fig. 1). Here the lineaments are developed in the Yakima Basalt of the Columbia River Group. These lineaments have commonly been interpreted as simple down dip drainage formed in a manner analogous to rills developed on a fresh soil slope.

The studies reported herein present a detailed analysis of the jointing in the Big

Summit Prairie area and its relation to local folds. These results are then compared to a similar analysis of lineaments in the Heppner area to show that a similar pattern exists with the same relation to local folds. On this basis, I argue that regional jointing is indeed present in the Columbia River Basalt over wide areas, and is a valuable aid to tectonic interpretation. However, these joints are probably rarely distinguishable from the plethora of cooling joints seen in individual outcrops. Thus they are not easily seen in the field, but instead must be studied on remote imagery of some kind.

As used in this paper, the term "lineament" refers to linear features mapped on air photos or other remote imagery. The origin of these must be demonstrated by independent data or arguments. In the Columbia River Basalts I separate regional from local joints on the basis that regional joints extend through more than one flow and beyond individual outcrops, whereas local joints are confined to a single outcrop and flow. A joint set is made up of subparallel regional joints.

Methods

Different kinds of imagery were used for lineament mapping in each study area during this investigation. In the approximately 1000 sq km studied around Big Summit Prairie both NASA U-2 false-color infrared photography (Flight 72-114) with stereo coverage and Landsat multispectral scanner imagery (frames 1004-18210 and 1076-18211) were available. Results on each are comparable and the U-2 data, originally at a scale of 1:120,000, is included herein (Fig. 2). In the approximately 3700 square kilometers studied in the Heppner area both Landsat imagery and Skylab photography were avail-

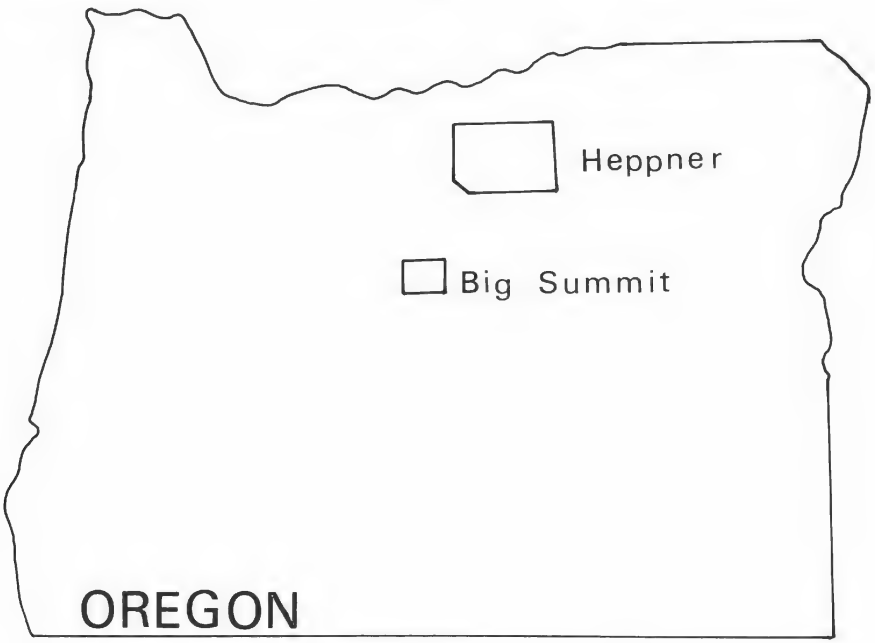

Figure 1. Location map of areas studied.

able and results from both are compared (Figs. 3 and 4). Landsat imagery (frame 1076-18204) at 1:500,000 of band 5 (0.6-0.7μ) and color reconstitutions of bands 4 (0.5-0.6μ), 5, and 7 (0.8-1.1μ) were used. The Landsat satellite system is discussed by Boeckel (1973). Side-lap stereo enhancement at 1:1,000,000 was also examined for the same bands. The results for the various formats were combined and only those lineaments which were mapped more than once are shown. A Skylab color photograph at a scale of about 1:125,000 taken on 4 August 1973 was used.

The lineament data acquired from the various kinds of imagery were compiled and plotted on rose diagrams showing total length of linear for each 5° interval. Individual

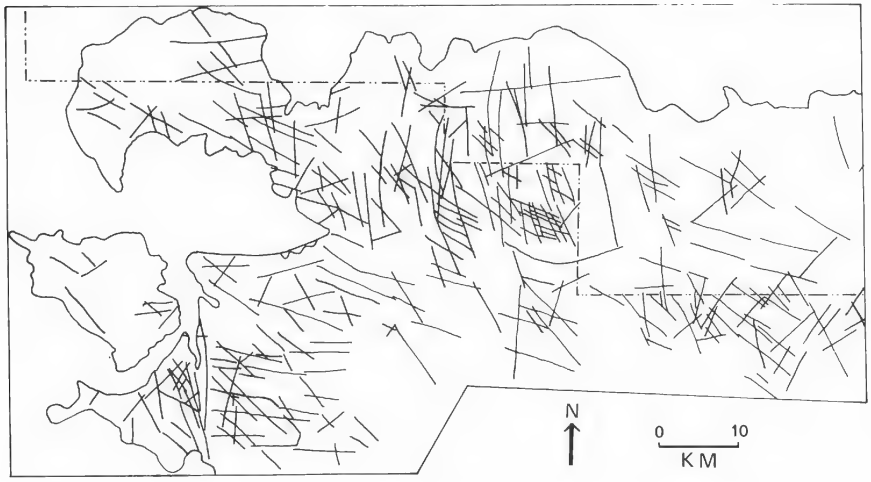

Figure 2. Lineament pattern in the Big Summit Prairie area, Oregon, mapped from NASA U-2 infrared photography (Flight 72-114).

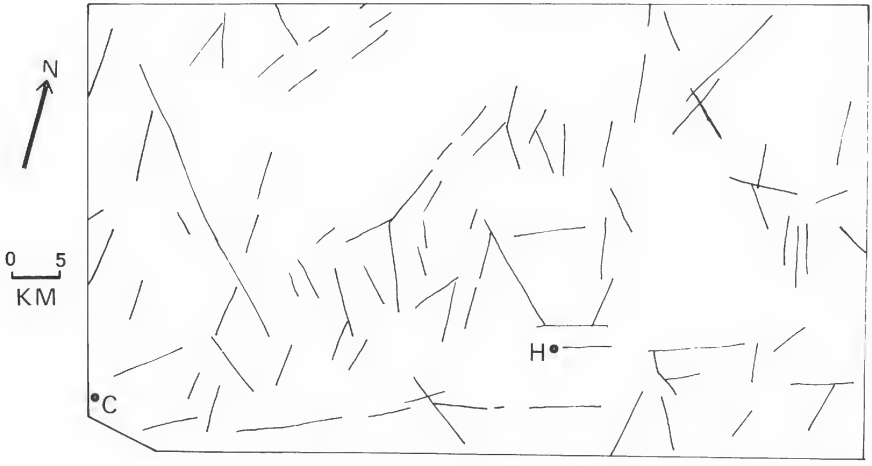

Figure 3. Lineament pattern in the Heppner area, Oregon, mapped from Landsat frame 1076-18204, bands 4, 5, and 7. H=Heppner and C=Condon.

peaks were selected by two averaging techniques. First, as shown on Figures 5 and 6, all peaks greater than the average length of linear were calculated from minimum to maximum and these are labelled in those instances in which they are greater than twice

Figure 4. Lineament pattern in the Heppner area, Oregon, mapped from Skylab photo of 4 August 1973. H=Heppner and C=Condon.

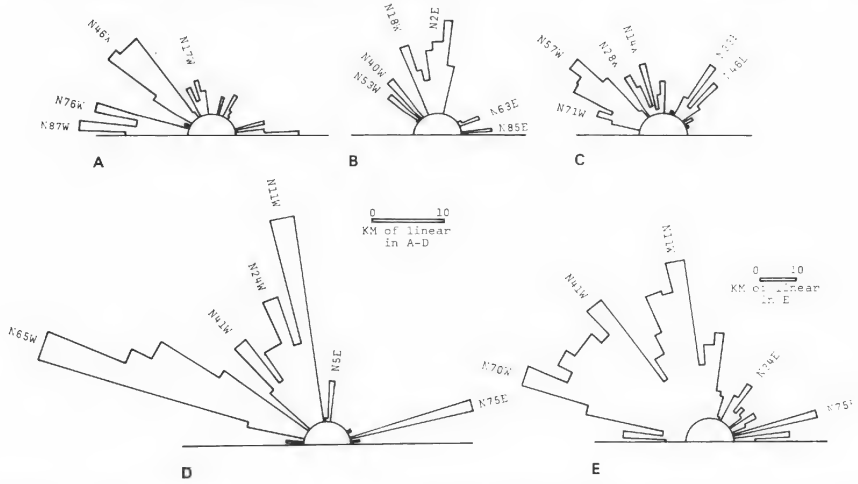

Figure 5. Rose diagrams of lineament patterns in Big Summit Prairie area. (A) 236 km of lineament in the southwest subarea. (B) 149 km of lineament in the north-central subarea. (C) 212 km of lineament in the northeast and southeast subareas. (D) 366 km of lineament in the northwest and south-central subareas. (E) Summary diagram of 910 km of lineament in the entire area.

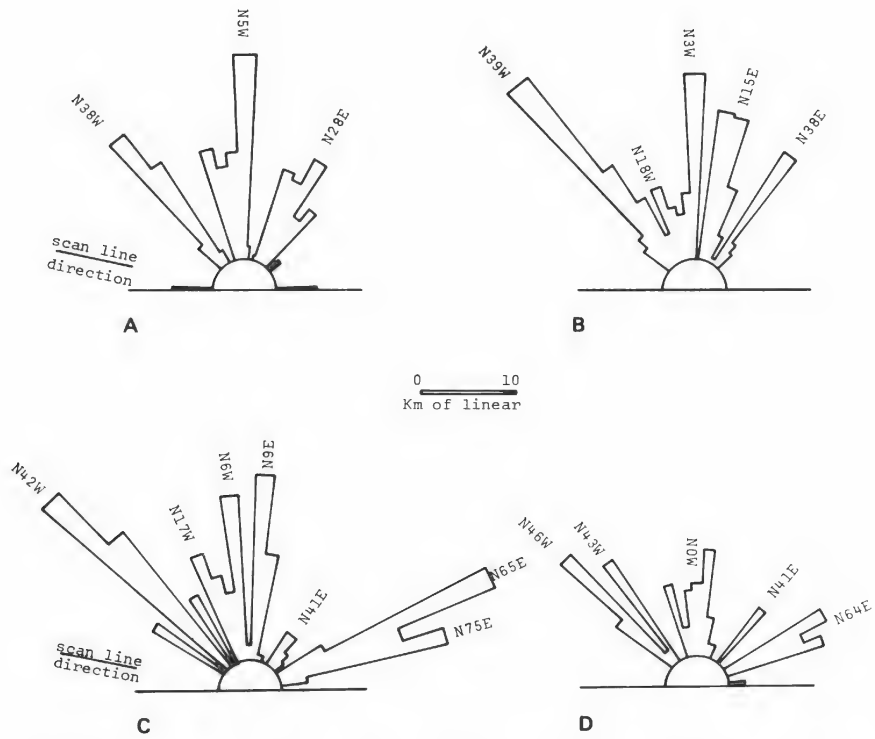

Figure 6. Rose diagrams of lineament patterns in the Heppner area. (A) 204 km of lineament in the northern subarea from Landsat imagery. (B) 471 km of lineament in the southern subarea from Skylab imagery. (C) 299 km of lineament in the southern subarea from Landsat imagery. (D) 195 km of lineament in the southern subarea from Skylab imagery.

the average (cf. Diamond and others, 1975). The relative size of the individual peak probably relates to uncontrolled variables such as rock dip, slope, and drainage trend, but all peaks are probably real. The total number of peaks found by this technique is probably increased by accidental minima resulting from the relatively small total number of linears involved. Second, on the assumption that some of the minima are accidental, the peaks are combined into a few major peaks for the purpose of tectonic interpretation.

Within each area the homogeneity of the results was tested by plotting rose diagrams of smaller subareas. For the Big Summit Prairie area six subareas were plotted (NW, NC, NE, SW, SC, SE). The NE and SE subareas and the NW and SC subareas showed no significant difference and are combined in Figure 5. For the Heppner area four subareas were plotted (NW, NE, SW, SE) for both Landsat and Skylab results. The two northern subareas and the two southern subareas showed no significant differences in pattern and are combined in Figure 6. No significant difference in pattern is recorded between the two kinds of satellite imagery used in the Heppner area.

Statistical results of the measurements are presented in Table 1. A few interesting

contrasts are observed. The average length of linear on the Landsat imagery is about 33 percent greater than on either of the other two formats and the density of lineament is much greater in the Big Summit Prairie area than on either format used in the Heppner area. Within the Heppner area the density is higher on the Landsat imagery than on the Skylab photo. These observations reflect two phenomena. More lineaments are

TABLE 1. Measurement Statistics.

	Heppner Area		Big Summit
	Landsat	Skylab	Prairie Area
Surface area	3700 km²	3700 km²	1000 km²
Imagery scale	1:500,000	1:125,000	1:120,000
Total number of lineaments	255	232	329
Total length of lineaments	1094 km	667 km	910 km
Average length of lineament	4.3 km	2.9 km	2.8 km
Density of lineament	0.30 km/km²	0.18 km/km²	0.91 km/km²

actually present in the Big Summit Prairie area than in the Heppner area, creating the main density contrast. This finding reflects the relatively thin Columbia River Basalt unit with moderate dips in which the joint pattern has been enhanced by landslide creep in the Big Summit Prairie area, in contrast to the thicker basalt of low dip and no sliding in the Heppner area. On the other hand, the difference in length of linear is an imagery artifact. The Landsat small scale imagery tends to make several separate subparallel lineaments be mapped as a single feature. When multiple lineaments are connected over short distances, a slight increase in lineament density occurs. It is important to note, however, that the lineament patterns are not affected; thus, the Landsat imagery provides as useful a set of data for tectonic interpretation (see data offered below) as does the larger scale imagery. Less time is needed to work with the Landsat material.

Results

In the Big Summit Prairie area the lineaments are known from field observation to be joints. Their presence was first recorded by Swanson (1969). As noted above, the Ochoco Mountains in Crook County are a tilted fault block and joints are abundant on the south facing dip slope (Lawrence, 1974). Landslide creep down this slope on underlying tuffs and tuffaceous sediments of the John Day Formation has opened the joints to erosion resulting in their dramatic topographic expression. These are regional joints which in some cases pass entirely through the Columbia River basalt unit and have an average length of 2.8 km. In individual outcrops they are indistinguishable from the innumerable local cooling joints that have purely local patterns. On the rose diagrams (Fig. 5) numerous individual peaks are present. These can be generalized into three main sets that are present in all subareas, and can best be seen in the summary diagram. In each subarea there is a central set, A, with two other sets, B and B′, arranged at about 30° on either side of A. The degree of development of the different sets varies, but all three are present in each case. In two subareas other sets are present. These general results are shown on Table 2 below.

In the Big Summit Prairie area, axes of open folds in the basalts trend about N45°E in most of the area, but rotate toward east-west in the north. Joint set A is oriented per-

pendicular to these fold axes with an overall N41°W trend. The rotation of the axes to the north of the area is reflected by the N18°W and N28°W trends of the joints in the NC and NE-SE subareas. Joint sets B and B′ are symmetrically oriented about 40° to each side of set A and the perpendicular to the fold axes. Thus joint set A is in the position of cross joints and sets B and B′ those of conjugate diagonal joints commonly developed in association with folds (Price, 1966; Dennis, 1967). Longitudinal joints along the fold axes are not developed.

TABLE 2. Orientations of Main Lineament Sets, Big Summit Prairie Area.

Subarea	Set B	Set A	Set B′	others
(A) SW	N84°W	N46°W	N17°W	
(B) NC	N47°W	N18°W	N 2°E	
(C) NE-SE	N57°W	N28°W	N 0°W	N39°W
(D) NW-SC	N65°W	N41°W	N11°W	N75°E
(E) All	N70°W	N41°W	N11°W	

These folds are present in much of north-central Oregon south of the Blue Mountain anticlinorium. Their axes trend northeasterly and they developed progressively from before the deposition of the Oligocene John Day Foundation until not long after the Picture Gorge basalts erupted at about 15 m.y. ago (Oles and Enlows, 1971; Baksi, 1972). The folds and related joints in the Big Summit Prairie area must have developed after the basalts and prior to the formation of the tilt block that forms the Ochoco Mountains in this area. The last motion on these faults was after the Rattlesnake Ignimbrite erupted about 6.4 m.y. ago (Davenport, 1971; Enlows and Parker, 1972). However, the Ochoco Mountains existed as a barrier to the ignimbrite so that much of the motion must be earlier (Enlows, pers. comm., 1976). The three joint sets, A, B, and B′, developed at approximately the same time as the folds—that is, toward the beginning of the period between 15 and 6.5 m.y. ago, or late Miocene to early Pliocene.

In the northeastern corner of the area, a northwest trending fold set is present that is more widespread to the east and northeast. According to Thayer and Wagner (1969), these folds developed in the early middle Pliocene. They are reflected in the NE-SE subarea (C on Fig. 5) by the joint set trending around N39°E, which would record cross joints to these folds (or perhaps tightly grouped diagonal joints). The joint set trending N75°E in the NW-SC subarea (D on Fig. 5) does not systematically relate to any other structures in the area except possibly the normal faults. (Fig. 7).

In the Heppner area the lineaments mapped have not previously been noted or discussed. They appear on the imagery as linear drainage segments, some of which cross drainage divides. The few known faults, such as those along Rock Creek near the west edge of the area, are expressed as such lineaments, which suggests that the linear segments are structurally controlled. The area is along the north to northwest dip slope of the Blue Mountain Anticlinorium. Dips are ½° to 3° (Newcomb, 1969) on this slope. Dendritic drainage such as characterizes homogeneous rock bodies is nowhere developed. If numerous faults were present, these would be discernible in the field from basalt stratigraphy. However, regional joints would not be distinguishable in outcrop from local cooling joints which have been shown (Shannon and Wilson, 1974) to have a random orientation. Just north of the Heppner area, regional joints are visible from low flying aircraft in a few places along the Columbia River where the basalts were

scoured by the Spokane flood during the late Pleistocene. Thus, the lineaments are believed to be sets of regional joints along which erosion proceeds preferentially.

Here three main lineament sets, A, B, and B′, can be distinguished even more clearly than in the Big Summit Prairie area. In the south half of the area a fourth set, C, is also present (Table 3). The differences between the Landsat and Skylab results are negligible. The three main sets, A, B, and B′, are similar to the sets with the same labels in the Big Summit Prairie area. The angle of separation is about 40° instead of 30° as is observed at Big Summit Prairie.

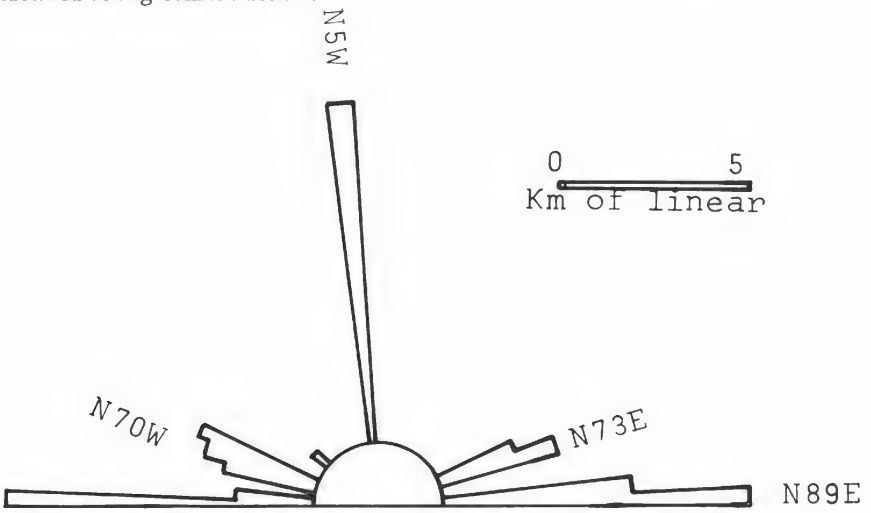

Figure 7. Rose diagram of normal fault trends in the Big Summit Prairie area.

Most folds in the Heppner area (Newcomb, 1970; Shannon and Wilson, 1973) have axes which trend approximately east-west. These are very broad, open folds that developed in the Yakima and Late Yakima Basalts of the Columbia River Group between 10 and 3.5 m.y. ago (Laursen and Hammond, 1974; Shannon and Wilson, 1973). Faults that developed simultaneously with the folds (Shannon and Wilson, 1973) trend about N35°-40°W. These are similar in trend and character to the strike-slip faults of the Warwick fault system to the northwest near Golden, Washington. The few folds with northwest trending axes may be draped over concealed faults of similar character. Lineament set A corresponds to a set of cross joints perpendicular to the east-west trending fold axes. Lineament sets B and B′ correspond to conjugate diagonal shear joints crossing the same folds. Thus, these lineaments are interpreted to be joint sets re-

TABLE 3. Orientation of Main Lineament Sets, Heppner Area.

Subarea	Set B	Set A	Set B′	Set C
(A) Landsat N	N38°W	N5°W	N28°E	
(B) Skylab N	N39°W	N3°E	N38°E	
(C) Landsat S	N42°W	N3°E	N41°E	N69°E
(D) Skylab S	N41°W	N0°E	N41°E	N64°E

lated to folding in the same manner as those at Big Summit Prairie, but may be somewhat younger in age.

Lineament set C is developed only in the southern part of the area and is nearly a single linear feature. It is developed at nearly right angles (70°) to set A, but is not a longitudinal joint system related to the folds in detail as it crosses fold axes. No local structures that correspond to it are known; but it does parallel the axis of the Blue Mountain anticlinorium.

Discussion

The results presented above demonstrate the existence of regional joint sets in the Columbia River Basalts that are of tectonic origin and significance. These are distinct from the cooling joints that are of purely local origin and are best analyzed from small scale imagery. The most prominent joints in the two areas examined in detail are cross and diagonal joints developed in relation to local folds. The trend of the cross joints, set A, parallels the direction of maximum compression, σ_1, and related shortening that generated the folds. Thus, the general trace of set A across each of the detailed study areas corresponds to the trace of σ_1 at the time of origin of the joints and associated folds.

The combined results of the study contribute to an elucidation of the late Cenozoic tectonic history of north-central Oregon (Fig. 8). In the Big Summit Prairie area the joints record a northwest trend to σ_1 in the late Miocene and early Pliocene. In the

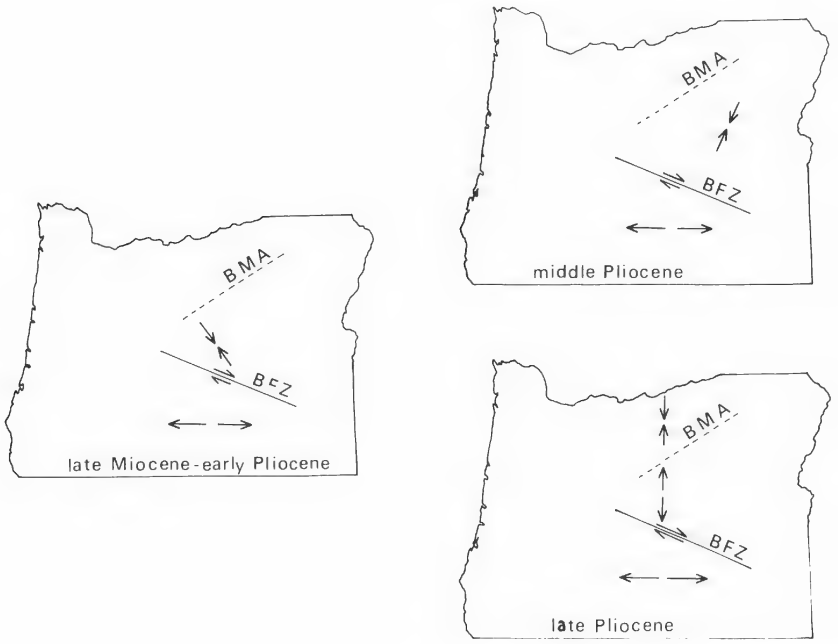

Figure 8. Distribution of Late Cenozoic stress fields in central Oregon. BFZ=Brothers Fault zone and BMA=Blue Mountain anticlinorium.

northeast corner of the area the lesser impress of a northeast trend to σ_1 of middle Pliocene age is present. Folds associated with this stress field are better developed east and northeast of the study areas. The tilted fault block structure of the Ochoco and Maury Mountains developed in the late Pliocene records a change to north-south extension. Probably simultaneously with but perhaps just after this last event, the joints of the Heppner area record a north-south trend to σ_1 in the late Pliocene in that area.

The north-central Oregon block under discussion here ends against the Brothers fault zone to the south. This fault zone is a right lateral strike-slip fault that has been active during the late Cenozoic period discussed above. (Lawrence, 1976). South of this fault zone is the Basin and Range province where approximately east-west extension has gone on for this entire period. The Brothers fault zone separates these two contrasting tectonic provinces and its motion accomodates the change in strain that occurs between them. Thus, during the last 15 m.y. north-central Oregon has experienced mainly compression and shortening with a strong north-south component simultaneous with the equally persistent east-west extension of southeastern Oregon.

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Extractable Soil Nutrients and Permafrost under Adjacent Forest Types in Interior Alaska[1]

Abstract

Soils in two adjacent forest stands in interior Alaska, one birch (*Betula papyrifera*) and the other black spruce (*Picea mariana*), were sampled in 2-cm increments to a depth of 50 cm. The soils had developed from the same parent material and were similar in slope and aspect. The soil had a thicker organic surface layer and was underlain by permafrost under spruce, but none was found under birch.

Although the mass of the organic layer under spruce was twice that under birch, only the total amount of K in that layer, and not N, P, or Ca, differed between the two sites. There were no differences in concentrations of NO_3, Ca, and K extractable with *N* NaCl between the spruce and the birch soils; NH_4 and PO_4 were significantly different. Because of low bulk density in the ice-rich permafrost under spruce, the total amount of extractable nutrients in the mineral soil was lower under spruce than under birch. More of the potentially unavailable nutrients N, P, and K were immobilized in the organic layers than in permafrost under the spruce.

Introduction

Interior Alaska forests are areally dominated by open, slow-growing black spruce (*Picea mariana* (Mill.) B.S.P.) on poorly drained sites, sites underlain by permafrost, and cool sites on north-facing slopes. Hardwoods, mostly paper birch (*Betula papyrifera* Marsh.) but also some aspen (*Populus tremuloides* Michx.), are also common; they occupy warmer sites or sites recently disturbed. The mosaic of vegetation is closely related to fire history, and these forests are frequently burned (Viereck, 1973).

An ideal scheme of forest succession after fire in the region includes changes from birch stands to black spruce stands with an understory of sphagnum mosses and finally to sphagnum bogs with scattered spruce(Heilman, 1966; Viereck, 1970). The active or seasonally thawed layer of soil above the permafrost is generally thickest in the earliest successional stages and decreases with time. This decrease is accompanied by a thickening of the organic surface layer (Heilman, 1966; Viereck, 1970). This ideal scheme is not always realized. Many spruce stands are replaced by spruce following fire, without intermediate stages of succession, depending on such factors as degree of disturbance and seed source. Hardwood stands are regarded as seral, however; barring disturbance, they are expected to succeed eventually to spruce (C. T. Dyrness, pers. comm., 1976).

Some work has been done on the relationship of soil properties to forest types in interior Alaska. Heilman (1966, 1968) examined differences in soil and foliar nutrient levels in a suite of stands corresponding to the successional sequence. He found that N, P, and K are deficient in the later stages of succession as nutrients become unavail-

[1]This work was conducted during the summer of 1975 while the author was a visiting scientist at the Pacific Northwest Forest and Range Experiment Station, Institute of Northern Forestry, USDA Forest Service, Fairbanks, Alaska 99701.

able in frozen or cold organic layers. He concluded that removal of moss by fire, and the subsequent deeper thawing of the underlying soil, concentrates available nutrients near the soil surface and thus improves productivity.

Troth *et al.* (1976) contrasted soil properties under aspen-birch and black spruce stands but without a specific successional orientation. They found significant differences in properties between the two groups and concluded that the differences indicated more rapid return of nutrient elements from the hardwood litter and by inference more rapid nutrient cycling in the hardwood stands. None of their stands had significant soil permafrost.

The purpose of this study was to compare soil properties under two adjacent forest stands, one hardwood and one spruce, selected to be as similar as possible in soil parent material, slope, aspect, and overstory age. Because the spruce stand was underlain by permafrost and the birch stand was not, the study was also to examine the interrelationships of permafrost with other soil properties at these two otherwise similar sites.

Methods

The two sites were on the Washington Creek Experimental Area of the U.S. Forest Service-Bureau of Land Management, about 48 km north of Fairbanks, Alaska. This area is near the center of the Interior Basin climatological province. Mean annual temperature is about -3°, with variations ranging from -50° to 35° C.

One site is a small paper birch stand (ca. 2000 m^2) in a matrix of black spruce. Basal area of paper birch is about 14 m^2/ha and of black spruce, 3 m^2/ha. The oldest birch on the site are about 140 years old; they are stump sprouts from an older stand. There is also a younger age class of birch that probably became established after a ground fire about 70 years ago. Bluejoint reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) is the dominant understory species, with lesser amounts of horsetail (*Equisetum sylvaticum* L.). There is a nearly complete absence of mosses on the forest floor.

The other site is a black spruce stand about 120 m away. This site is part of a "finger" of spruce that extends downslope, apparently having escaped the last fire about 70 years ago. Basal area of spruce is 23 m^2/ha. No other overstory species are present. Decomposed birch stumps are scattered in the stand, indicating that birch had been an earlier component. The spruce are also about 140 years old, originating after the same fire as the oldest birch. The forest floor is covered by mosses, primarily *Pleurozium schreberi* (Brid.) Mitt. and *Hylocomium splendens* (Hedw.) B.S.G., with a few patches of *Sphagnum. Calamagrostis* and *Equisetum* are also present.

The soil underlying both sites has been mapped as a Saulich silt loam—a loamy, mixed, nonacid Histic Pergelic Cryaquept (Furbush and Schoephorster, 1974). The dominant slope direction is southeast, with the birch stand sloping SSE, and the spruce stand sloping ESE. The stands differ slightly in slope gradient—10 percent in the spruce stand and 14 percent in the birch.

Soils were sampled in mid-July 1975. Three pits were dug in each stand and the mineral soil was described and sampled in 2 cm thick, fixed volume increments to a depth of 50 cm. The samples were returned to the laboratory, weighed, and dried for moisture determination. Concentrations of NO_3, NH_4, PO_4, Ca, and K from each sample were determined in a *N* NaCl extract (1:10, wt:vol). Analyses were done with a Technicon Autoanalyzer (mention of products by name does not constitute an endorsement

by the U.S. Department of Agriculture) for NO_3, NH_4, and PO_4, and by atomic absorption spectroscopy for Ca and K.

The surface organic layers at seven locations in each stand were sampled with a constant area sampler (180 cm^2). Samples were separated into 01 and 02 horizons, dried, weighed, and ground through a coarse (10-mesh) sieve. Samples were analyzed by extraction, as were the mineral samples (but with a 1:10, vol:vol ratio); and by ashing at 525° C and determining major elements through emission spectroscopy in an acid solution of the ash. Nitrogen was determined by the micro-Kjeldahl method (Bremner and Tabatabai, 1972). Analyses of variance and multiple-range tests were used in analysis of the resulting data (Hogben *et al.*, 1971; IMSL, 1972; Weisberg and Koehler, 1976).

Results and Discussion

Soil Morphology

Soils at both sites had dark brown silt loam A horizons about 8 cm thick, with moderate fine granular structure; mottled grayish brown silt loam B horizons with weak fine platy structure; and mottled dark grayish brown C horizons, also with weak fine platy structure, that had developed in silty loess that is high in mica.

The soils differed, however. At the spruce site, the mossy organic layer was about 20 cm thick; at the birch site, it was only about 10 cm thick. Ice-rich permafrost occurred at the spruce site at 30 cm, near the bottom of the B22 horizon, but no permafrost occurred at the birch site to at least 150 cm. Finally, there were indications of cryoturbation (mixing by frost action) in the pedon at the spruce site. Streaks of black, apparently organic-rich material convoluted through the upper parts of the soil. These morphologic expressions of freeze-thaw movements, however, were not as extensive as those described by Pettapiece (1975) for an area farther east, in the Lower Mackenzie Basin.

Soil Physical and Chemical Properties

The soils at the two sites were similar in particle-size distribution and pH. All horizons were silt loam, with about 70 to 75 percent silt and 10 percent clay. At both sites, the pH of the surface was about 4.1, and of the C horizon, 6.3

Differences in bulk density in the soils were significant for site and for depth. Mean bulk density under birch (1.25 g/cm^3) was significantly higher than under spruce (0.96 g/cm^3). Most of the difference, however, was in the lower B22 and the C horizons or the permafrost zone (below 30 cm) (Fig. 1a).

Bulk density differences were related to moisture content (Fig. 1b). In the permafrost zone under spruce, up to 70 to 80 percent of the soil volume was ice; in the seasonal freeze-thaw zone (at ca. 15 cm), about 40 percent was ice. This volume was similar to that occupied by water immediately above the frozen zone. Moisture differences were statistically significant for both site and depth.

Cryoturbation, because it causes irregular distribution of organic matter through the soil, could potentially affect levels of extractable nutrients. Troth *et al.* (1976) found a high correlation between soil carbon and cation exchange capacity in similar soils. The result of cryoturbation could be higher variability in nutrient distribution in soil under spruce than under birch, where cryoturbation did not occur. I compared the pooled variance for moisture content, bulk density, and each nutrient between sites. Only

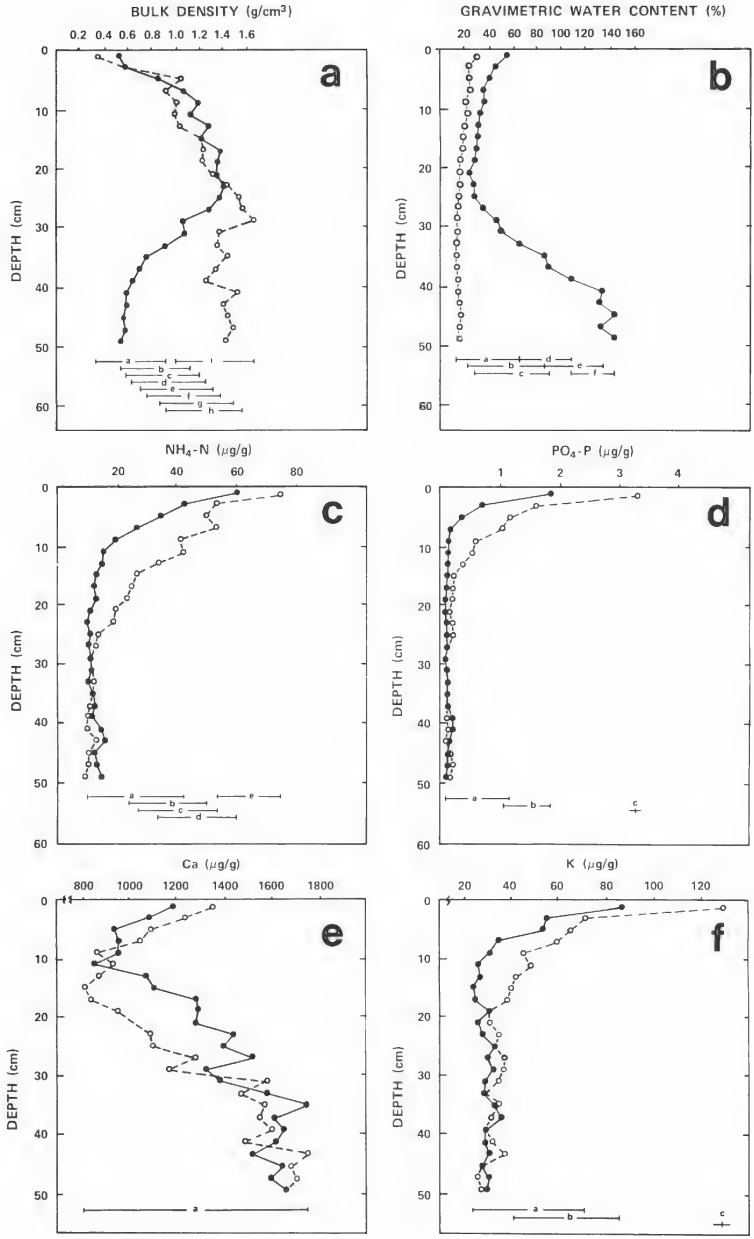

Figure 1. Change in soil properties with depth under adjacent forest stands in interior Alaska. Permafrost was present in the spruce stand at 30 cm. Each point represents three observations. Zones delimited at bottom of each figure are not significantly different at 0.05 level. 1a, bulk density; 1b, gravimetric soil water; 1c, NH_4-N; 1d, PO_4-P; 1e, Ca; 1f, K. Solid line, spruce; dashed line, birch.

moisture content had significantly higher variance under spruce; all other properties had equal variances and so cryoturbation did not cause detectable variation in measured soil properties.

The results of the nitrate analyses will not be presented in detail. Although there were significant nitrate differences with depth, there were no significant differences between sites. The mean nitrate-nitrogen concentrations were low at both sites (about 0.6 μg/g).

Ammonium nitrogen concentrations were significantly different among depths and between sites. Soil under the birch stand had a higher mean concentration (25.2 μg/g) than did that under the spruce (18.2 μg/g). The differences between the sites, however, were almost wholly within the upper 20 cm of the mineral soil, and not in or near the permafrost (Fig 1c).

Extractable PO_4-P, Ca, and K also showed similar relationships (Fig. 1d, 1e, 1f). Where differences were significant between sites (PO_4-P), the differences were primarily near the surface and not in the permafrost. These near-surface differences led to nearly twofold higher P concentrations under birch (0.47 μg/g) than under spruce (0.24 μg/g).

I initially hypothesized that sharp changes in levels of nutrients near the top of the permafrost and/or higher concentrations within the permafrost could occur with succession. As permafrost encroached into the active layer, recycling nutrients would be immobilized. The rooting volume within the active layer would also be reduced, leading to greater depletion of nutrients in that layer and to the hypothesized changes. The data indicated neither marked discontinuities with depth nor differences between sites in extractable nutrients near or within the permafrost (Fig. 1). The interaction of nutrient cycling and permafrost formation does not lead to irregular nutrient distributions with depth.

Although our measures of concentration may be indicative of nutrient availability, the total mass or quantity of nutrients is also important for birch and spruce. A small quantity of nutrients may potentially be exhausted by vegetation, even if present at high concentrations. The higher concentrations (primarily near the surface) and the higher bulk density (primarily in the lower horizons) under birch lead to a greater mass of extractable nutrients in soil under birch. Differences were statistically significant for all nutrients.

The organic surface layers are also important. Heilman's work (1966, 1968) emphasized that differences in nutrient level between early and late successional stages were related to the organic surface. Troth *et al.* (1976) found more Ca in the organic layers under aspen-birch than under spruce and more K under spruce. I did not find a large difference in mass of nutrients in the organic surface between the spruce and the birch site. Although the mass of the organic layers under spruce (10,000 g/m^2) was significantly higher than that under birch (5,600 g/m^2), concentrations of major nutrients were negatively correlated with that mass so that only K showed significantly more in the organic layers under spruce than under birch.

The analytical procedure separated four categories of nutrients: mobile and immobile within the organic layer and mobile and immobile within the mineral soil. Nutrients extractable with *N* NaCl from the organic layer were considered mobile, and those not extractable were considered immobile. In the mineral soil, those extracted

from the active layer were considered mobile, and those within the permafrost were considered immobile. Although there was no significant difference in the total mass of N, P, and K in the organic layers plus the upper 50 cm of the mineral soil between the spruce and birch systems (Ca was higher under birch), there were differences in partitioning among the four categories (Fig. 2).

Extractable N in the NH_4 form (total quantity in the NO_3 form was only about $0.3 g/m^2$ at each site) was present in both the mineral soil and the organic layers. The bulk of the N, however, was in a non-extractable form (determined by the micro-Kjeldahl method) in the organic layers (Fig. 2).

Almost no P was extracted with *N* NaCl from the mineral soil (Fig. 2). Although it is not a strong extractant, the quantity extracted by NaCl was lower in a pilot study but correlated (r=0.82) with that extracted by Bray's No. 1 solution. By far the majority of the available (extractable) P is in the organic layers, with an additional large amount fixed in the organic layers.

Calcium apportioning is much different from that of N and P. Mineral soil is the prime repository of calcium, with little present in the organic layers, either extractable or fixed. The amount fixed in permafrost under spruce is also high (Fig. 2).

Potassium behavior is intermediate to that of the other elements that have been dis-

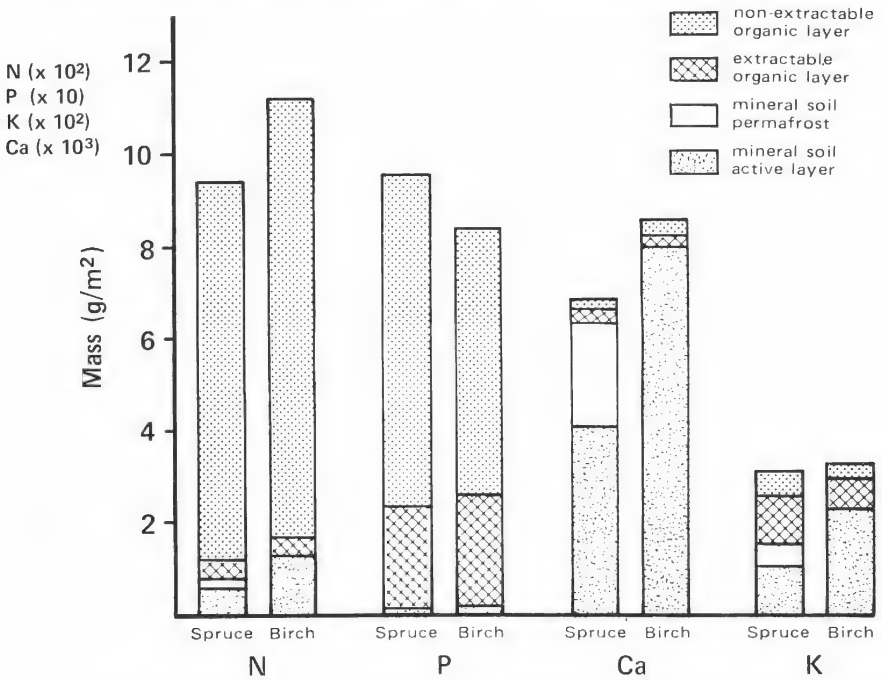

Figure 2. Mass of nutrients in organic layers and upper 50 cm of mineral soil under adjacent forest stands in interior Alaska. Categories include that portion extractable from organic layers with *N* NaCl and that not extractable, and that extractable with *N* NaCl from the active layer of the mineral soil and that extractable from the permafrost. Nitrogen extractable as NH_4 and P as PO_4; nitrate N was also extracted but was present in negligible amounts.

cussed. Potassium is present in similar amounts in the organic layer and in the mineral soil (Fig. 2), with a portion fixed in both the organic layer and in permafrost.

The birch and spruce sites I studied were similar in slope and aspect, the soils underlying them were formed from the same parent material, and the overstories became established after the same fire, about 140 years ago. The sites differed appreciably in vegetation characteristics and in some soil properties. The major soil differences were a thicker organic layer and permafrost under spruce; minor soil differences included slightly higher levels of extractable nutrients in the mineral soil under birch. These differences are typical of those in similar forest stands in interior Alaska, and these data fit well with other observations (Troth *et al.*, 1976). The differences are analogous to changes that occur with succession from seral hardwoods to black spruce in interior Alaska (Heilman 1966, 1968).

As succession proceeds, elements that are at low levels and potentially limiting, such as N, P, and K, are cycled by the vegetation; they accumulate in the increasingly thick organic layer (Heilman, 1966 & 1968). The thickness of the active layer of the soil decreases, also immobilizing nutrients. Even though I found that the organic layer was significantly thicker under spruce, only the mass of K, but not that of N or P, was higher under spruce. This result has also been found in similar stands that varied more widely in age (Troth *et al.*, 1976). The only element immobilized to any degree by permafrost was Ca; Heilman (1968) did not find Ca to be deficient in the successional series of stands he studied.

Because the soil differences found are relatively transient, I interpret them to be caused by, rather than to be the cause of, the vegetation differences observed. Whether these soil differences arose only during the present generation of vegetation or more likely during a continued occupancy by similar vegetation types is difficult to determine. The lack of significant differences in concentrations of extractable nutrients in the permafrost compared with concentrations in a similar permafrost-free soil indicates either that the permafrost formed a relatively short time ago or that it has little effect on nutrient cycling.

In the two systems I studied, soil differences alone are not adequate to explain fully the present situation. The interrelationships between the soil and vegetation systems on the sites are interwoven with the history of the site in such a way that neither vegetation nor soil can be evaluated in a cause-effect relationship (Jenny, 1961). The interactions within the vegetation-soil system and their response to disturbance create antecedent conditions for the next system that occupies the site: determination of such interactions in a historical context is certainly difficult, and probably impossible.

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Autumn Populations of Spiders and Other Arthropods in an Urban Landfill

Abstract

The study site, on Union Bay, Seattle, Washington, is a former wetland modified by dumping and earth fill. The present flora, mainly moss and grass clumps, dates from 1971. Analysis of Berlese funnel extracts from turf samples shows very low arthropod diversity and absence of taxa of low dispersal ability. In contrast to older grassland, Collembola outnumber mites by 3.7:1. The spider fauna of both ground and field layers is dominated by an introduced Theridiid, *Enoplognatha thoracica* (Hahn). The only centipeds are parthenogenic species of *Lamyctes* (Henicopidae). The site is set aside for ecological research so these data can be compared with future changes in the fauna.

The Montlake landfill is an area of about 53 ha on the east part of the University of Washington campus, adjoining Union Bay of Lake Washington and not exceeding 7.6 m in elevation. Originally natural wetland, the area was used from 1926 to 1965 as a dumping site for organic and inorganic refuse, with a surface layer of earth fill. The study site is the area of most recent fill, comprising 23 ha in the southeast part of the main landfill. In 1971 this area was covered with excavated mineral soil, primarily Vashon Till from the southwest part of the campus, and graded; the present vegetation and fauna dates from that time. Parking lots, housing, playfields, and some small remnants of the original marsh surround the site. The University currently plans to maintain the area in its present state for ecological research (Jones and Jones, 1976).

On 31 October and 4 and 6 November 1976, I collected turf samples (1160, 890, and 930 cm^2 in area) at random sites in the south central part of the study area. They were taken to a depth of 5-10 cm, below which the compacted till offers little habitat for microarthropods. The claylike till substrate (0 to 4 m thick) supports in most places a 1 to 2.5 cm deep covering of moss, primarily *Ceratodon purpureus* (Hedw.) Brid. Vascular plants include sparse clover (*Trifolium repens* L.) and plantain (*Plantago lanceolata* L.), with clumps of grass, mainly *Agrostis alba* L. and *Agropyron repens* (L.) Beauv. Other plants are present in relatively very small numbers. There is essentially no humus except within the bases of grass clumps, which occupy 30 percent of the area of the turf samples. Growth is curtailed in some parts of the landfill by methane escaping from subsurface decomposition, but this curtailment is not noticeable in the sample area.

The samples were processed in a large, standard Berlese funnel with a 150-watt light bulb as heat source. Doubtless the extraction efficiency was significantly below 100 percent as a result of mortality in the turf. Although this factor and the small number of samples limit the quantitative significance of the data, they may still be useful for comparison as changes in the landfill are observed over time. Table 1 pre-

sents the numerical results in terms of numbers of individuals per square meter.

Each taxon enumerated includes 10 or fewer species, often only one. Such low diversity is to be expected for such an austere and newly created habitat. Comparable studies of older and richer grassland and pasture habitats, such as those of Salt *et al.* (1948), Hairston and Byers (1954), and Morris (1968), show significant numbers of arthropod taxa of low dispersal ability, such as Diplopoda, Symphyla, Pauropoda, Geophilomorpha (soil centipeds), Chelonethida (pseudoscorpions), and Protura, none of which were found in the Montlake landfill, though present in nearby older habitats.

TABLE 1. Arthropod Populations in the Montlake Landfill.

Taxon	Population per m^2 Mean	Range
INSECTA		
Total Collembola	48,828	29,930-60,936
Poduridae	9,222	1,629-21,033
Entomobryinae	690	169-1,367
Isotominae	25,799	14,736-34,413
Tomocerinae	31	11-65
Sminthuridae	13,104	4,080-25,562
Thysanoptera	39*	0-78
Hemiptera		
Lygaeidae (1 species)	1,122	86-2,847
Other Hemiptera	122	65-155
Homoptera		
Aphididae	38	22-69
Cicadellidae	30	11-45
Coleoptera adults		
Staphylinidae	182	124-293
Other Coleoptera	118	78-180
Coleoptera larvae	135	0-237
Lepidoptera larvae	78	0-183
Diptera adults	9*	0-17
Diptera larvae	494*	452-535
Hymenoptera adults	14*	11-17
ARACHNIDA		
Total Araneida	221	124-366
Total Acarida	13,331*	9,793-16,868
Phalangida (juvenile **Phalangium opilio** Linne)	20	0-43
CHILOPODA		
Total Lithobiomorpha	117	52-213

*Counted only in the first and third samples.

The authors noted above and many others studying older grasslands found mites to be the largest component of the fauna, outnumbering Collembola in ratios from around 2:1 to the extreme of 17.3:1 found by Hairston and Byers (1954) in a disused pasture in Michigan. In the Montlake landfill the Collembola outnumbered mites by about 3.7:1, and in addition their population density is distinctly greater than that found for most long-established grassland habitats. This is in accord with the finding of Baweja (1939) that during re-invasion of sterilized soil, Collembola soon surpassed their original numbers; mites did not readily regain them. In the present case this effect may reflect both the greater dispersal ability of Collembola and the small depth of habitable soil available to mites. Few previous studies have enumerated species of mites, but Hairston and Byers (1954) found 79 species, of which 20 in the Oribatoidea formed 69 percent of the total number of mites. Two to three of the 10 or fewer mite species in the Montlake landfill were Oribatoids, a similar proportion, but these formed less than 10 percent

of the total number. The lack of success of Oribatoid mites may be another reason for the low abundance of mites as a whole in the landfill habitat.

The spider fauna is dominated by juvenile, mainly penultimate, *Enoplognatha thoracica* (Hahn), Theridiidae ($147/m^2$), identified with reference to adults collected in spring at the study site. This circumstance is unusual and probably temporary; Erigonidae usually predominate in temperate ground spider faunas. Other spiders include *Erigone olympias* Crosby and Bishop, Erigonidae ($29/m^2$); juvenile *Xysticus* sp., Thomisidae ($15/m^2$); juvenile *Pirata* sp., Lycosidae ($12/m^2$, but some probably escaped when samples were taken); indeterminate Theridiids and Erigonids, each $7/m^2$; and juvenile *Clubiona* sp., Clubionidae ($4/m^2$). In the first two species, sex ratios were nearly 1:1.

Non-quantitative sweep samples, taken at the study site on 28 May 1975 by N. Cimino and on 6 November 1976 by me, show the composition of the spider fauna in the field-layer. These samples are equally dominated by *Enoplognatha thoracica*, followed by *E. ovata* (Clerck), *Tetragnatha* spp., and *Lepthyphantes tenuis* (Blackwall), with occasional specimens of *Xysticus* sp., *Tibellus* sp., *Erigone olympias*, *Montilaira ksenia* (Crosby and Bishop), and *Theridion bimaculatum* (Linné). *Enoplognatha thoracica* is known from two localities in southwestern Washington but may have been introduced on the landfill, since it seems to be absent elsewhere in the vicinity. A European species, its only previous North American records are from towns in Northwestern Oregon (Levi, 1957). The other spiders appear to have invaded the landfill from the surrounding area. The *Pirata* sp. probably came from the small areas of undisturbed marsh along Union Bay, offshore and southeast of the landfill, where the ground spider fauna also includes *Erigone* spp., *Pachygnatha* sp., and others.

All the Lithobiomorph centipeds are Henicopidae, mainly *Lamyctes* sp. near *pinampus* Chamberlin ($113/m^2$), with occasional *L. fulvicornis* Meinert. Most *Lamyctes* populations are parthenogenic, and indeed all of these were females or juveniles. Parthenogenesis is thought to enhance greatly dispersal ability in *Lamyctes* (Eason, 1964, p. 22). This occurrence would explain their abundance on the landfill, though Lithobiidae are much more common in the surrounding area.

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Karyotype of the Red Fox, Vulpes vulpes L., in Alaska

Abstract

The chromosomal number in the red fox, *Vulpes vulpes* L., from central Alaska varied from 37 to 39 (2n=34+3-5 m). In cells from bone marrow, macrochromosomes were constant at 34 and microchromosomes ranged in number from 3 to 5, per cell, in the one male and one female studied. Karyograms from both animals are shown. The characteristics of the karyotype were found to correspond closely to those described in the literature about animals from localities in Eurasia and in mideastern North America.

Introduction

The diploid number of chromosomes in the red fox, *Vulpes vulpes* L., has been determined from animals from various localities in Eurasia, but not including the arctic and subarctic regions of Siberia. In North America, the geographic origins of animals studied, when stated, have been within the mideastern part of the continent. A comparison of the chromosomal characteristics of red foxes in northwesternmost North America seemed desirable, not only because of the great distance separating this region from those where foxes have been studied previously, but also because the animals probably are derived from a population that inhabited Beringia during the last (Würm) glacial period. Findings in red foxes from central Alaska are reported here.

Methods and Materials

Two foxes, *Vulpes vulpes alascensis* Merriam, a male and a female, were captured 5 and 11 km northwest of Fairbanks, respectively. An hour after intraperitoneal injection of a 0.05 percent solution of colchicine, marrow was collected from the femur and sternum, held 20 minutes in hypotonic sodium citrate, and fixed and stained in acetic orcein or in Carnoy's solution and Giemsa blood stain. G-banding of chromosomes was obtained following Seabright's (1972) method, using trypsin and Giemsa stain. The chromosomes in 100 cells from the male fox and 50 cells from the female were counted, and idiograms for comparison were prepared from photographs of 8 cells from the male and 6 from the female. Measurements were recorded of the non-banded complements. The banded chromosomes were matched by evident patterns. The Y-chromosome was selected by inspection.

Results

Male. (2n=34+3-5 m). From 37 to 39 chromosomes were present, depending on the variable number of microchromosomes. The number of macrochromosomes was con-

stant at 34. In 100 cells, 12 contained 37 chromosomes (3 microchromosomes + XY +32 large autosomes); 81 contained 38 (4 microchromosomes + XY +32); and 7 cells had 39 (5 microchromosomes +XY +32). The largest autosomes were about 6μm in length (metaphase). The X was identified as submetacentric, about 3μm long (metaphase), with indistinct banding. The Y-chromosome was subtelocentric, and not markedly different from some of the microchromosomes. Four of the latter appeared to be subtelo- to acrocentric, but when five were present in the complement, the odd one had the appearance of a dark dot. G-bands were not distinct or bright in the Y nor in the microchromosomes, but darker areas distally on the long arms were sometimes noted in the best preparations. G-banded chromosomes from the male are shown in Figure 1.

Figure 1. Giemsa-banded chromosomes of *V. vulpes*, male, central Alaska: 2n=34+4 microchromosomes.

Female. (2n=34+3-5 m). As in the male, the diploid number ranged from 37 to 39, with the macrochromosomes constant at 34. In 50 cells, 4 contained 37 chromosomes (3 microchromosomes +XX + 32); 41 contained 38 (4 microchromosomes +XX + 32); and 5 cells had 39 (5 microchromosomes + XX + 32). Figure 2 shows the chromosomes from one cell with 39 chromosomes; the 32 large autosomes have been arranged in three groups, pair-numbers 1-5 with arm-ratios ranging from 1.01 to 1.50, numbers 6-13 with ratios of 1.51 to 2.20, and numbers 14-16 with ratios from 2.70 to 2.90. The arm-ratio of X ranged from 1.60 to 1.80. For convenience, the karyogram follows the arrangement adopted by Lin *et al.* (1972).

Discussion

Comparison of our findings with those of Gustavsson (1964), Moore and Elder (1965), Gustavsson and Sundt (1967), Sasaki *et al.* (1968), Vogt and Arakaki (1971), Low and Benirschke (1972), and Renzoni and Omodeo (1972), and with the quinacrine fluorescent karyograms published by Lin *et al.* (1972), indicates that karyotypic differences among the macrochromosomes are slight and probably reflect methods of prep-

aration. Our karyogram as well as that of Lin *et al.* (1972) would correspond closely to a rearrangement of the karyogram of *V. vulpes* from Iran published by Hsu and Benirschke (1974). Evidently *V. vulpes* [including *V. fulva* (Desmarest)] has a diploid number of 34 macrochromosomes plus a variable number of microchromosomes, with the total count ranging from 34 to 40-41.

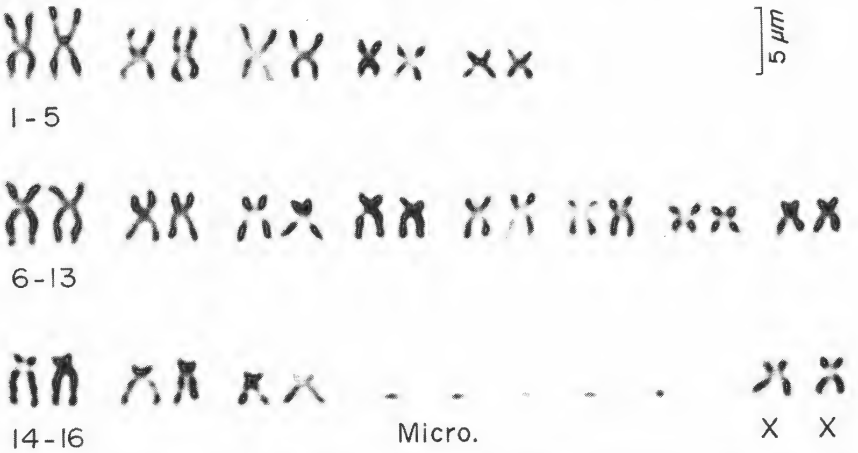

Figure 2. Chromosomes of *V. vulpes*, female, central Alaska: 2n=34+5 microchromosomes. Giemsa blood stain.

The major differences in karyotype are related to the number of microchromosomes present, but since such elements have been found to vary in most red foxes (within as well as among individuals) from localities widely separated geographically, this, too, is a constant karyotypic character of the species. The significance of the microchromosomes and their variance is unknown. Rather than being in the process of elimination from the genome, as was suggested by Gustavsson and Sundt (1967), the microchromosomes may exert a positive influence (Renzoni and Omodeo, 1972). Ward *et al.* (1972) suggested that the number of micro-elements may be positively correlated with size and vitality of the individual. The foxes that we studied were collected at a time of relatively high species population density in central Alaska.

V. vulpes is one of several species of mammals of palaearctic origin that first appeared in North America during the penultimate (Riss/Saale) glacial period (Kurtén, 1966; Rausch, 1977). Its status as a holarctic species, established on macromorphologic grounds by Churcher (1959) and others, is supported by the karyologic data.

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Microbial Ecology of Olympic Hot Springs

Abstract

The ecology of Olympic Hot Springs in Olympic National Park was studied through laboratory and field observations from September 1972 through October 1973. Olympic Hot Springs was found to be a meteoric-low salinity hot spring with a temperature maximum of 47°C and a pH of 9.2. The warm, alkaline waters supported a biological community similar to those of other alkaline hot springs.

Introduction

The hot spring environment provided an interesting system for study since it probably had existed throughout the time that life had been evolving on earth. The organisms found growing under these thermal conditions helped to reveal the extent to which evolution had been pushed. From an ecological point of view, studies were simplified by the limited speciation and short food chains found in these sites. Possible beneficial applications of hot spring research include potential for prediction and control of the effects of thermal pollution in aquatic environments.

The role of temperature as an environmental factor and the uniqueness of the hot springs ecosystem has been reviewed by Castenholz (1969) and Brock (1970). The limnology of Ohanapecosch Hot Springs in Mount Rainier National Park has been described by Stockner (1968). The studies described herein resulted from the monitoring of certain of the physical, chemical, and biological properties of Olympic Hot Springs from September 1972 through October 1973.

Olympic Hot Springs is located in the north-central portion (48° N) of Olympic National Park at an elevation of 900 m. The study area (Fig. 1) covered 50 m^2 and was isolated from the main hot springs area where human activity had had minimal effect on the ecosystem. The site was located on a north-facing slope and consisted of a narrow main stream 35 cm wide by 20 cm deep, fed by two springs (sites 1 & 2), and a pool located on the east side of a small island separating the pool from the stream. The pool was fed by a spring which flowed up from the bottom (site 5). The source at site 1 flowed from the hillside, falling 1 m to the head of the stream channel (site 3): the stream at site 2 flowed down a rocky slope for 3 m to the head of the channel. The stream and pool joined 8 m downstream from the hillside sources forming a circulating out-flow pool (site 10) which drained over a steep slope to the Elwah River.

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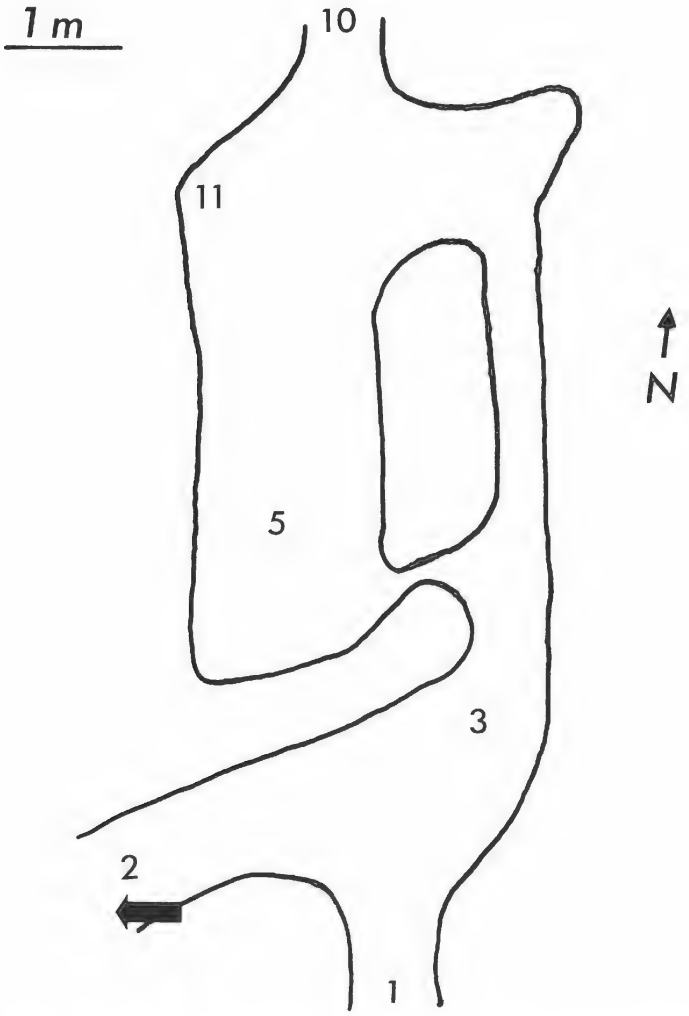

Figure 1. Olympic Hot Springs study area (numerals refer to sampling sites). The arrow indicates the location of the pipe used to divert the source water in the manipulation experiment.

Methods and Materials

Field observations and samples were taken monthly at designated sites marked by numbered wooden stakes. Temperature and dissolved measurements were made using a portable temperature, salinity, altitude compensated/oxygen meter (YSI model 51 A, Yellow Springs Instrument Co., Yellow Springs, Ohio). A Taylor pH comparator (VWR Scientific) was used for pH determinations.

Water samples for chemical analyses were collected in sterile 1 liter polyethylene

bottles. One liter of water from each of sites 1, 2, and 10 was collected, fixed with chloroform, and stored on ice for phosphate analysis. One liter of water from the same sites was collected and placed on ice for use in the remainder of the chemical analyses.

Biological samples from selected sites were collected and stored in sterile glass jars and transported to the lab for cultural studies at ambient temperature.

The blue-greens from the algal mat were isolated in uni-algal culture for taxonomic classification on Allen's medium (1968) and Castenholz's Medium D (1969). The organisms were isolated and maintained at 40°C under 750 ft candles illumination.

A photosynthetic bacterium from site 5 and two filamentous bacterial types (one from site 2 and the other from site 11) were maintained in the laboratory by means of a modified "Winogradsky column" (Castenholz, 1972) with a thermal gradient from 32°C to 45°C.

In an effort to determine the in situ relationship between the algal mat and the filamentous bacterium on the slope between sites 2 and 3, a manipulation experiment was attempted. The source waters at site 2 were diverted by inserting a short length of PVC pipe into the source and channeling the water for approximately 0.5 m before it flowed from site 2 to site 3. This manipulation caused the water temperature on the slope between site 2 and 3 to decrease by several degrees.

Results and Discussion

Chemical and physical limnological data from Olympic Hot Springs are summarized in Table 1. The monthly temperature, pH, and dissolved oxygen were constant throughout the observation period with only minor seasonal fluctuations occurring in temperature ($\pm$ 1°C) and dissolved oxygen ($\pm$ 1 mg l^{-1}). The data indicate that Olympic Hot Springs was a meteoric-low salinity hot spring according to the classification of Castenholz (1969). This characterization is consistent with the meteoric rather than volcanic origin of the thermal waters (N. Anderson, pers. comm.).

The temperatures of the source waters at sites 1 and 2 were 42°C and 47°C, respectively. The water at site 5 flowed up from a spring at the bottom of the pool, with

TABLE 1. Chemical composition of Olympic Hot Springs waters (all values given in ppm unless otherwise indicated).

	Site 1	Site 2	Site 10
conductivity (μmhos cm^{-1})	290	300	290
turbidity (JTU)	0.49	1.50	0.68
NH_3	0.53	0.78	0.55
NO_3	0.12	0.12	0.16
PO_4	0.10	0.11	0.11
sulfates	32	25	30
Cd	0.004	0.004	0.004
Cr	0.006	0.006	0.006
Cu	0.01	0.01	0.01
Ni	0.008	0.008	0.017
Pb	0.10	0.10	0.10
Zn	0.001	0.019	0.001
Ca	1.20	1.80	1.44
Mg	0.07	0.06	0.06
pH	9.2	9.2	9.2
temperature (°C)	42	47	41

temperature measured at 47°C and a dissolved oxygen content of 0.5 mg l^{-1}. The condition of the pool was anoxic.

The microbial flora of Olympic Hot Springs was found to be similar to previously described alkaline hot springs (Stockner, 1968; Castenholz, 1969; Brock, 1970). The stream supported a mat of blue-green algae (also known as cyanobacteria [Stanier, 1974]) 3-4 cm thick which was made up of *Phormidium laminosum*, *Oscillatoria trebriformis*, and *Synechoccus lividus*. The underside of the mat lacked the heterotrophic flexibacteria found in algal mats of hot springs of higher temperatures (J. Bauld. pers. comm.). The rocky slope from site 2 to the head of the stream was covered by *Sphaerotilus natans*, a unicellular, rod-shaped bacterium enclosed in a sheath which gives the colony a white filamentous form.

In the pool area the algal mat was limited to the top centimeter of the pool's surface because of the anoxic conditions below. At the bottom of the pool, in areas not shaded by the algal mat, deep red patches of the photosynthetic purple sulfur bacterium *Chromatium violascens* were observed. The filamentous bacterium *Thiothrix nivea* was found along the margins of the pool where the water temperatures were cooler (30-35°C).

During April and May of 1973 it was noted that the flow from a cold spring which fed into the pool along its margin had diminished. This change resulted in a temperature increase from 33°C to 43°C. Accompanying this increase was a steady decline in the *Thiothrix* population until a level of approximately 40°C was reached; at this point, the organism disappeared from the system. Its thermal maximum had apparently been exceeded.

As a result of the manipulation of the source at site 2 the water temperature decreased from 47°C to 43°C with little effect on the overall flow rate. Accompanying the decrease in temperature was a change in the community structure between site 2 and the head of the stream channel. Within a month of the manipulation, the algal mat had spread up to the diversion point while *S. natans* had disappeared. Within a month after the flow pattern was restored to normal and the temperature increased to 47°C, the algal mat had receded to its original position in the stream and *S. natans* recolonized the slope below site 2.

These results suggest several alternative hypotheses: 1) growth of the algal mat was limited to temperatures below 47°C while that of *S. natans* is optimal at about 47°C; 2) increased competition by the blue-green algae may have lead to the demise of *S. natans* at the lower temperature; or 3) *S. natans* may excrete inhibitory factors which limit the growth of the blue-green algae, and it is only when *S. natans* is limited by the lower temperature that the blue-green can spread unchecked.

Apart from the microbial community described above, the only other major contributor to the hot springs community which was observed was the grazing fly *Paracoenia turbida* (Diptera:Ephyridae) which is common in hot springs with temperatures of 30-40°C (Brock, 1970; Collins *et al.*, 1976). These grazers contribute to the ecosystem through their feeding and excretory processes and their mechanical effects on the algal mat which allow greater gas and nutrient exchange (Brock, 1970).

These observations indicated that a biological community had developed which was typical of an ecosystem with the chemical and physical properties of Olympic Hot Springs. The members of the hot springs community were found to be living very near

their thermal limits so that small changes in temperature led to rapid changes in the species diversity of the ecosystem. Community stability seemed to be dependent upon the constant physical and chemical properties found there.

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Planktonic Microcrustacea of the Lower Snake River Drainage

Abstract

Sixteen lakes and ponds in the Lower Snake River drainage were sampled over a one-year period for species and numbers of microcrustacea, primary phytoplankton productivity, chlorophyll content, water temperature, pH, total alkalinity, oxygen content, and light levels. Collection sites varied from highly alkaline "pot holes" in the west to low alkalinity oligotrophic lakes in the east. Other plankton samples were also taken to provide additional distributional notes.

Fifty-one species of Copepoda and Cladocera were collected from the drainage. This collection included 33 species of Cladocera in 16 genera, 9 species of cyclopoid copepods in 5 genera, and 2 genera of calanoid copepods with 9 species. The cyclopoid, *Cyclops bicuspidatus thomasi*, and the cladoceran, *Chydorus sphaericus*, were the most numerous and widespread microcrustaceans. Four species of cyclopoid copepods, one diaptomid, and six species of Cladocera dominated the fauna in this system. Community structure, density, and dominance in the microcrustacea are also discussed.

Introduction

Although the position and importance of the microcrustacea in the aquatic ecosystem is well established, there is still much to be learned of their systematics and distribution. This paper is the initial report of work conducted from August 1975 through June 1976 concerning the distribution and community structure of the cyclopoid and calanoid Copepoda and Cladocera in lakes, ponds, and reservoirs of the Lower Snake, Palouse, Tucannon, and Clearwater Rivers in Washington and Idaho.

Pacific Northwest distributional studies include the following: British Columbia (Carl, 1940), British Columbia and Alberta (Anderson, 1971, 1974), Central Basin of Washington (Whittaker and Fairbanks, 1958), Grand Coulee and adjacent area (Kiser, 1939), Spokane area (Hewitt and Gustafson, 1947), Western Washington (Wilson, 1972), Washington and Idaho Lakes (Kemmerer, Bovard, and Boorman, 1923), Upper Snake River (Forbes, 1898), British Columbia (Clemens, Rawson, and McHugh, 1939), McNary Reservoir on the Columbia River (Scarola, 1968), southern Oregon lakes (Tash, 1971), and mountain lakes of Idaho (Wissmar and Rabe, 1970; Parr, Rabe, and Wissmar, 1968). Several of these papers by Whittaker and Fairbanks (1968), Hewitt and Gustafson (1947), Wissmar and Rabe (1970), and Parr, Rabe, and Wissmar (1968) list microcrustacea from a few lakes in the study area, but no comprehensive work on the copepods or cladocerans of the Lower Snake drainage has been published before this time.

Sampling Locations

The area sampled includes the drainage of the Lower Snake River from and including the Clearwater system to the Columbia River (Fig. 1). Topography of the area varies from dry, rolling sagebrush of Washington's Central Basin to wet, coniferous forests of the Bitterroot Range of eastern Idaho. Precipitation ranges from less than 20 cm

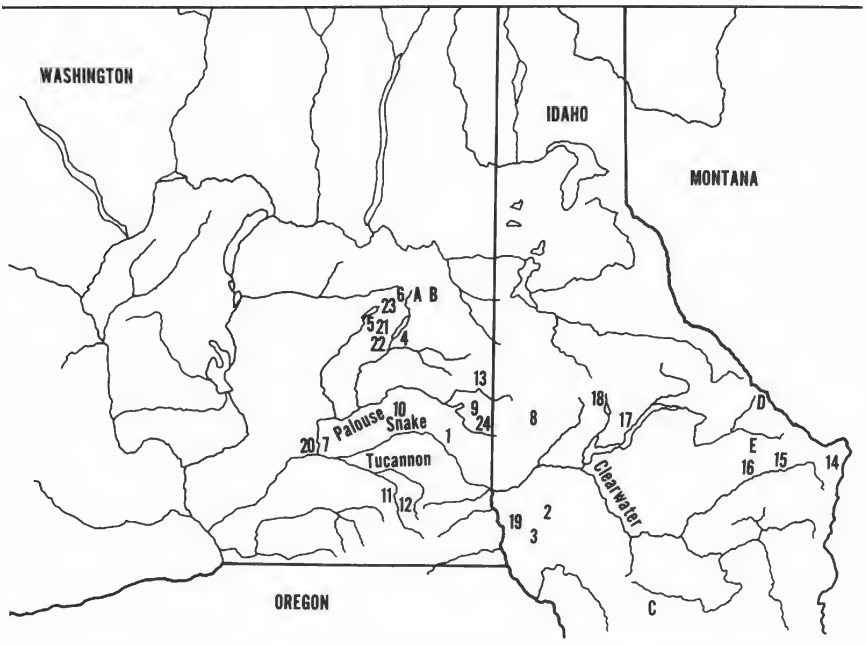

Figure 1. Sampling locations. Numbers correspond to those in text. Letters indicate collection records of other workers as follows: A and B—Hewitt and Gustafson (1947), C—Espinosa (pers. comm.), D—Rabe (pers. comm.), and E—Wismar and Rabe (1970).

per year in the west to over 162 cm in the eastern part of the drainage. As expected with such a large geographic area, the range of physical, chemical, and biological parameters is great (Table 1).

TABLE 1. Physical and chemical properties of sampled waters.

Statistic	Variables						
	C^{14} (mg $C/m^3/hr$)	Temp (°C)	Chlorophyll (mg/m^3)	pH	Alkalinity (g $CaCO_3/m^3$)	Oxygen (ppm)	Light (μamp)
Range	154.4-0.0	22.5-0.5	27.95-0.0	9.8-5.6	535.6-11.5	15.8-0.9	275-0
Mean	10.08	13.21	2.61	7.6	79.4	6.7	45

Sampling was conducted at the following locations:

1. Lower Granite Reservoir, Wawawai Landing, Whitman Co., WA., T 13 N, R 3 E, Sec. 3.
2. Lapwai Lake, Winchester State Park, Winchester, Lewis Co., ID., T 33 N, R 2 W, Sec. 6.
3. Soldiers Meadow Lake, Nez Perce Co., ID., T 33 N, R 3 W, Sec. 32.
4. Rock Lake, Whitman Co., WA., T 19 N, R 40 E.
5. Sprague Lake, Adams Co., WA., T 20 N, R 38 E.
6. Williams Lake, Spokane Co., WA., T 21 N, R 41 E, Sec. 7.

7. Lyons Ferry, Lower Monumental Reservoir, Franklin Co., WA., T 13 N, R 37 E, Sec. 19.
8. Spring Valley Reservoir, Latah Co., ID., T 40 N, R 3 W, Sec. 17.
9. Smoot Hill Pond, Smoot Hill Preserve, Washington State University, Whitman Co., WA., T 16 N, R 44 E, Sec. 34.
10. Pampa Pond, Whitman Co., WA., T 15 N, R 39 E, Sec. 17.
11. Spring Lake, Columbia Co., WA., E 10 N, R 41 E, Sec. 21.
12. Rainbow Lake, Columbia Co., WA., T 10 N, R 41 E, Sec. 21.
13. Garfield Juvenile Fishing Pond, Whitman Co., WA., T 17 N, R 45 E, Sec. 6.
14. Lily Lake, Idaho Co., ID., T 38 N, R 15 E.
15. Whitehouse Pond, Whitehouse Campground, Clearwater National Forest, Idaho Co., ID., T 37 N, R 13 E.
16. Unnamed pond formed by U.S. Highway 12 cutting off old bend in Lochsa River, 53 km upstream from the confluence of the Lochsa and Selway Rivers, Idaho Co., ID., T 36 N, R 12 E.
17. Dworshak Reservoir, Clearwater Co., ID., T 38 N, R 1 E.
18. Elk River Reservoir, Elk River, Clearwater Co., ID., T 40 N, R 2 E.
19. Waha Lake, Nez Perce Co., ID., T 33 N, R 4 W, Sec. 9.
20. "Borrow pit" approximately 1 km downriver from Lyons Ferry State Park, Franklin Co., WA., T 13 N, R 37 E, Sec. 19.
21. Unnamed roadside pond 5.3 km south on Washington 23 from intersection of Washington 23 and Interstate 90, Lincoln Co., WA., T 21 N, R 39 E, Sec. 32.
22. Unnamed roadside pond 8.3 km south on Washington 23 from intersection of Washington 23 and Interstate 90, Whitman Co., WA., T 20 N, R 38 E, Sec. 16.
23. Negro Creek, Sprague, Lincoln Co., WA., T 21 N, R 38 E, Sec. 24.
24. Unnamed roadside pond at junction of Kamiak Butte Road and Washington 27, Whitman Co., WA., T 16 N, R 45 E, Sec. 15.

Methods

Plankton samples were taken with a 12 volt pump and 12.5 cm plankton net of #25 bolting cloth. Samples were fixed in 5-10 percent formalin and returned to the laboratory where they were transferred to 70 percent ethanol with 1 ml of glycerin added for permanent storage. Systematic identifications were made using keys by Brooks, Wilson, and Wilson and Yeatman in Edmondson (1959). Dissections were performed in glycerin and permanent mounts made with glycerin jelly. Volume of water filtered was calculated from the known rate of pumping and length of time pumped. Crustacean density figures were determined by one of two methods. Either total counts were made for each species or 1 ml aliquots were removed with a Hensen-Stemple pipette and counted in a Sedgwick-Rafter cell. Counts of 1 ml aliquots were repeated until 100 specimens of the most abundant species were tallied or until the average number of specimens per species did not change appreciably from one aliquot to the next. With the known sample volume and volume filtered, numbers of individuals per cubic meter of habitat water were calculated.

When depth was greater than 10 m, three levels were sampled: 1, 5, and 9 m. In lakes of 3-5 m, samples from 1 m below surface and 1 m above bottom were taken and in waters of less than 3 m only the 1 m depth was sampled. Each collection included

plankton sample and data regarding temperature, oxygen content, primary productivity determination, alkalinity, pH, light measurement, and chlorophyll determination. Temperature and oxygen were measured with a Yellow Springs YSI Oxygen Meter. A Sargent pH meter Model PBL was used for in-field determinations, and measurements of light reaching sampling depths were made using a Whitney underwater photometer. Methods for determining alkalinity are those outlined by Lind (1974). Procedures by Vollenweider (1974) and Lind (1974) were used in the C^{14} method for assessing primary phytoplankton productivity. Chlorophyll determinations were made using procedures by Lind (1974).

A total of 40 samples were taken in summer, 1975, 36 in winter, 1975-76, and 26 in spring, 1976.

Results and Discussion

Fifty-one species of Copepoda and Cladocera were identified from 24 lakes and ponds (Table 2). This number included 5 genera of cyclopoid copepods with a total of 9 species, 2 genera of calanoid copepods including 9 species, and 33 species of Cladocera in 16 genera.

TABLE 2. Copepoda and Cladocera from Lower Snake River drainage.

Species	Collections # of	Locations	Density of (x) samples in #/m³
Cyclopoida			
Cyclops bicuspidatus thomasi Forbes 1882	63	1-9, 11, 13, 17, 19	4018(56)
C. vernalis Fischer 1853	13	1, 7, 9, 11-13 20-22, 24	540(8)
C. varicans rubellus Lilljeborg 1901	4	9, 10	673(4)
Paracyclops fimbriatus poppei (Rehberg) 1880	2	1, 17	13(1)
Tropocyclops prasinus mexicanus Kiefer 1938	2	23, 24	—
Eucyclops agilis (Koch) 1838	12	9-13, 18, 22	167(9)
E. speratus (Lilljeborg) 1901	2	8, 23	300(1)
E. prionophorus Kiefer 1931	1	2	14(1)
Macrocyclops albidus (Jurine) 1820	17	2, 3, 8, 10-13, 15, 17, 18, 22, 24	343(11)
Calanoida			
Epischura nevadensis Lilljeborg 1889	3	4	113(3)
Diaptomus novamexicanus Herrick 1895	19	2, 5, 8, 19, 23	2977(15)
D. forbesi Light 1938	6	3, 13	267(5)
D. nudus Marsh 1904	7	3, 8	321(6)
D. ashlandi March 1893	9	4	1834(9)
D. sanguineus Forbes 1876	1	9	938(1)
D. eiseni Lilljeborg 1889	1	21	38(1)
D. sicilis Forbes 1882	3	21, 22	462,210(2)
D. leptopus Forbes 1882	1	22	—
Cladocera			
Daphnia schodleri Sars 1862	26	1-6, 19, 21, 23	12,413(20)
D. rosea Sars 1862 emend. Richard 1896	19	1-3, 5, 7, 11, 17, 19	3040(18)
D. pulex Leydig 1860 emend. Richard 1896	9	2, 4-6, 9, 22, 23	3480(6)
D. galeata mendotae Birge 1918	27	1, 2, 4-8, 17, 19	1822(25)
D. ambigua Scourfield 1947	2	1, 17	6(1)

TABLE 2. Continued

D. middendorffiana Fischer 1851	3	17, 20, 21	4329(2)
Bosmina longirostris (Muller) 1785	15	1, 5-7, 12	4044(11)
B. coregoni Baird 1857	13	3, 7, 17-19, 23	2765(8)
Ceriodaphnia quadrangula (Muller) 1785	5	3, 13, 16, 21, 24	110(2)
C. lacustris Birge 1893	11	2, 6, 10, 11, 22	4801(10)
C. reticulata (Jurine) 1820	11	1, 3, 6, 8, 13, 15, 19	3893(9)
C. laticaudata Muller 1867	3	11, 17	274(3)
C. pulchella Sars 1862	6	10, 19, 21	1944(6)
C. acanthina Ross 1897	1	2	—
Simocephalus serrulatus (Koch) 1841	3	12, 14, 18	140(1)
S. expinosus (Koch) 1841	1	11	1000(1)
S. vetulus Schodler 1858	9	9-11, 20, 21, 23, 24	4179(7)
Diaphanosoma leuchtenbergianum Fischer 1850	4	4, 7	409(4)
D. brachyurum (Lieven) 1848	1	15	—
Alona karua King 1853	1	18	47(1)
A. costata Sars 1862	3	11, 16	442(2)
A. guttata Sars 1862	11	1, 10-12, 16, 17, 21	486(6)
A. affinis (Leydig) 1860	1	4	17(1)
Alonella excisa (Fischer) 1854	1	10	20(1)
Graptoleberis testudinaria (Fisher) 1848	1	12	—
Leydigia quadrangularis (Leydig) 1860	3	2, 6, 19	44(3)
Leptodora kindtii (Focke) 1844	5	4, 5, 7	413(5)
Scapholeberis kingii Sars 1903	5	10, 14, 16, 17, 19	1471(1)
Holopedium gibberum Zaddach 1855	1	17	59(1)
Eurycercus lamellatus (Muller) 1785	4	6, 16, 18, 24	327(2)
Pleuroxus denticulatus Birge 1878	4	1, 11, 12	398(2)
Macrothrix laticornis (Jurine) 1820	1	1	28(1)
Chydorus sphaericus (Muller) 1785	53	1, 3-14, 16, 18-24	4936(44)

For the cyclopoids, the most significant new distributional information was the collection of *Eucyclops prionophorus*, the first record of this species from the Northwest. *Eucyclops speratus* has previously been recorded by Anderson (1974) in western Canada and was collected during this study at locations 8 and 23. *Tropocyclops prasinus mexicanus* was also taken for the first time in the Pacific Northwest, but whether this is a different subspecies from the *Cyclops prasinus* recorded by Carl (1940), Whittaker and Fairbanks (1958), and Kemmerer, Bovard, and Boorman (1923) has not been determined.

Of the Diaptomidae, the most noteworthy occurrence in the Lower Snake drainage is that of *Diaptomus shoshone* reported by Whittaker and Fairbanks (1958). If this indeed was the species collected in the Rock Lake area, Whitman Co., WA., these records are unusual. *Diaptomus shoshone* is said to inhabit only high altitude waters and records of it in shallow, high salinity waters have lately been attributed to *Diaptomus*

nevadensis (Anderson, 1974). It was not collected during the present investigation.

In addition to these records (Table 2), Hewitt and Gustafson (1947) reported *Bosmina longirostris* and *Cyclops bicuspidatus* in Badger Lake and *Daphnia longispina* and *Diaptomus sicilis* at Chapman Lake, Spokane Co., WA., both within the present study area. In addition, some work has been reported on high altitude lakes of Idaho. Espinosa (pers. comm.) lists *Daphnia rosea* from Crystal, Mirror, Upper, and Lower Wiseboy Lakes; *Macrocyclops albidus* from Crystal and Lower Wiseboy; *Cyclops vernalis* from Mirror Lake; *Diaptomus lintoni* from Crystal and Lower and Upper Wiseboy; *Diaptomus arapahoensis* from Crystal and Mirror Lakes; and *Diaptomus shoshone* from Upper Wiseboy. These lakes lie in the Buffalo Hump area of the Nez Perce National Forest, Idaho Co., ID., Lat 45°38′ N, Long. 115°41′ W. Rabe (pers. comm.) lists *Diaptomus shoshone* and *Diaptomus arapahoensis* from Upper Steep Lake, Clearwater Co., ID., T 41 N, R 12 E. Wismar and Rabe (1970) found *Diaptomus lintoni*, *Daphnia rosea*, *Cyclops* sp. and *Holopedium amazonicum* in Tin, Copper, Silver, and Gold Lakes, Shoshone Co., ID., T 42 N, R 9 E (Fig. 1).

Three-fourths of the microcrustacean species were present in no more than five locations while only four (*Cyclops bicuspidatus thomasi*, *Cyclops vernalis*, *Macrocyclops albidus*, and *Chydorus sphaericus*) were present in 10 or more sites. Several species have larger numbers in the "# of collections" column of Table 2 as a result of collecting the same species at different depths and over several seasons from the same waters. The four most widespread species accounted for 34 percent of the 429 occurrences, and the 39 least numerous species also totaled 34 percent.

The number of microcrustacean species comprising the communities at each site ranged from 0-4 cyclopoids, 0-2 calanoids, and 0-10 cladocerans with a total of 1-13 microcrustacean species per collection. The average number of cyclopoid copepod species per lake was 1.66; diaptomid copepods, 1.26 (in lakes where they were found); and cladoceran species, 3.5 for a total of 5.68 species per site. These figures are computed from the number of species per lake or pond per collection period. When compositions are averaged without regard to lake or season, the number of copepod species dropped to 1.85, Cladocera to 2.79, and total to 4.64.

These averages are similar to those reported by several other workers. Anderson (1974) found in western Canadian waters the mean number of copepods to be 2.35 and the mean for cladocerans, 2.66. Pennak (1957) reports from several sources an average of 2.7 copepod and 2.8 cladoceran species in 42 lakes scattered throughout the world. Helzer (1974), studying zooplankton population dynamics and productivity in five Nebraska reservoirs, found microcrustacean communities composed of 2.26 copepods and 3.07 cladocerans; and Patalas (1964) reports averages of 2.6-6.5 species, depending on altitudinal zone and dissolved solids content, in 52 Colorado lakes.

Although there were scattered instances of closely related species being taken in the same sample, one was almost always numerically dominant. For the cyclopoids, the dominant species comprised 83.6 percent of the total number of copepods and 67.9 percent of the microcrustacea when it was the overall dominant species. When a calanoid was the dominant copepod, it accounted for 81.7 percent of the copepods and 77.7 percent of the microcrustacea when it was the overall dominant. The dominant cladoceran made up 79.2 percent of the Cladocera and 72.0 percent of the microcrustacea when it was the dominant crustacean plankter. These figures are similar to those reported by Pennak

(1957) and Patalas (1964). Table 3 indicates the numerically dominant species of microcrustacea and the number of times dominant.

Average density figures for the different species varied from less than $10/m^3$ to over $400{,}000/m^3$. This latter figure was caused by the presence of *Diaptomus sicilis* in numbers approaching $1{,}000{,}000/m^3$ on one occasion at location 21 (Table 2). Density figures in Table 2 were often based on fewer samples than listed in the "# of collections" column since some species were collected from locations where no quantitative data were taken. Average densities for the cyclopoids (as a whole) were $2837/m^3$ and for the calanoid copepods, $1611/m^3$. Mean density for the Cladocera was $3750/m^3$ with the *Daphnia* density averaging $4167/m^3$ (Table 4). The numeric dominance of the Cladocera over the calanoids is difficult to understand in light of their similar size and feeding habits. Armitage and Smith (1968) found the same density relationship and its reverse and suggest some form of interaction in food competition between the two.

TABLE 3. Dominant microcrustacean species.

Species	Number of times dominant
Cyclopoida	
Cyclops bicuspidatus thomasi	22
Eucyclops agilis	2
Calanoida	
Diaptomus ashlandi	9
D. novamexicanus	3
D. sicilis	1
Cladocera	
Bosmina coregoni	2
B. longirostris	2
Ceriodaphnia lacustris	1
C. pulchella	1
C. quadrangula	1
C. reticulata	2
Chydorus sphaericus	19
Daphnia galeata mendotae	9
D. schodleri	7
Scapholeberis kingii	1

TABLE 4. Microcrustacean densities by collection period.

Collection period	Densities in number/m^3		
	Cladocera	Calanoida	Cyclopoida
1	3950	1901	1777
2	2475	1424	4749
3	4825	1507	1846
Average	3750	1611	2837

Conclusion

The planktonic microcrustacean fauna of the Lower Snake River system is dominated by four cyclopoid copepods, one diaptomid, and six cladoceran species. The cyclopoid, *Cyclops bicuspidatus thomasi*, and cladoceran, *Chydorus sphaericus*, are the most numerous and widespread microcrustacea. Community structure is comparable to that found by Anderson (1974) in Canada, Pennak (1957) worldwide, and Helzer (1974) and Patalas (1964) in the United States. The average lake or pond without diaptomids contained two cyclopoid copepods and four Cladocera, and the average lake with diapto-

mids contained two cyclopoids, one diaptomid, and four Cladocera. Even though several species of copepods or Cladocera may exist together, one species is almost always numerically dominant over the other species of the same group. Cladocera were present in the highest average densities: they were almost 2.4 times more numerous than the calanoids which occupy the same trophic position.

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Debris Removal and Its Effects on Sedimentation in an Oregon Coast Range Stream

Abstract

The removal of large organic debris obstructing anadromous fish passage in a Coast Range stream in Oregon accelerated downcutting of previously stored sediments. As a result, turbidity and suspended sediment levels increased during several storms after debris removal. Streamflow eroded more than 5,000 m^3 of sediment along a 250 m reach the first winter after debris removal. Therefore, fisheries managers who want to remove debris jams from streams must consider the stored sediments that will be scoured from the stream beds and deposited downstream.

Introduction

In small forest streams, large organic debris—capable of deflecting or locally reducing streamflow velocities—significantly affects physical characteristics such as channel form and local stream gradients. This observation is particularly true in the Pacific Northwest where headwater streams draining forest ecosystems often have debris loadings of 0.3 to 7.4 metric tons (t) per 10 m of channel length (Froehlich, 1973).

Large debris can markedly influence a stream's ecosystem. Frequently, large stable debris provides diverse habitats for fish and other organisms. It may also slow the routing of fine organics through the stream system, thus increasing the opportunity for biological degradation. However, in other instances debris creates a physical barrier that prevents anadromous fish from passing to upstream spawning gravels (Swanson *et al.*, 1976).

Spatial distribution as well as total quantity of debris significantly affects channel characteristics. Debris accumulations reduce streamflow in a channel and can thereby reduce the rate at which a stream dissipates energy. Consequently, the sediment-transporting capabilities of individual stream reaches also are affected. For example, stored sediment can be readily seen upstream from debris in a channel system while pools form directly downstream.

Debris can accumulate from a variety of natural processes including active earthflows, soil creep, and blowdown. Slope failures may result in debris avalanches that cascade debris and sediment down a hill to be deposited within a channel system. As streams undercut their banks, sediment and streamside vegetation enter the channel. These processes also may be accelerated by forest operations, particularly clearcutting on steep, shallow soils and road construction in unstable terrain (Swanston and Swanson, 1976). In addition, forest operations often directly add debris to streams.

Fishery managers planning to remove instream debris dams face a difficult decision. They must consider not only how this action will benefit fish passage, but also how debris removal will change channels and the load of suspended sediments. Although rates of sediment transport can be expected to change after debris removal, the mag-

nitude and rate of change often are unpredictable. The variability in amount and distribution of debris, channel characteristics, expected flow levels, particle size distributions, amount of stored sediments, and methods of debris removal all influence the final outcome.

In recent years, debris removal from headwater streams has become a tool used increasingly for meeting streamside management objectives. Yet the effects of debris removal seldom are documented. Consequently, this study (1) assessed the effects of debris removal on stream turbidity and sediment loads and (2) evaluated changes in channel geometry after debris removal.

Study Area

In the early 1960s, roadbuilding and logging began in the Mill Creek drainage approximately 3 km northwest of Alsea, Oregon. During the flooding that occurred throughout much of western Oregon and Washington in 1964-65, several debris accumulations became established in Mill Creek. Logging subsequently continued in the Mill Creek drainage. Road construction and logging immediately adjacent to the stream increased the chances for organic debris to enter the channel. As a result, debris continued to accumulate from 1965 through 1974. By 1975, several large debris accumulations (Fig. 1) had formed along Mill Creek, blocking upstream migration of anadromous fish.

During the summer of 1975, these large debris dams were removed in conjunction with a timber sale in the Mill Creek drainage. Cable yarding was used to remove some debris, and other sections were cleared by tractors and hand crews.

The section of Mill Creek with the debris accumulations (Fig. 1)— characterized

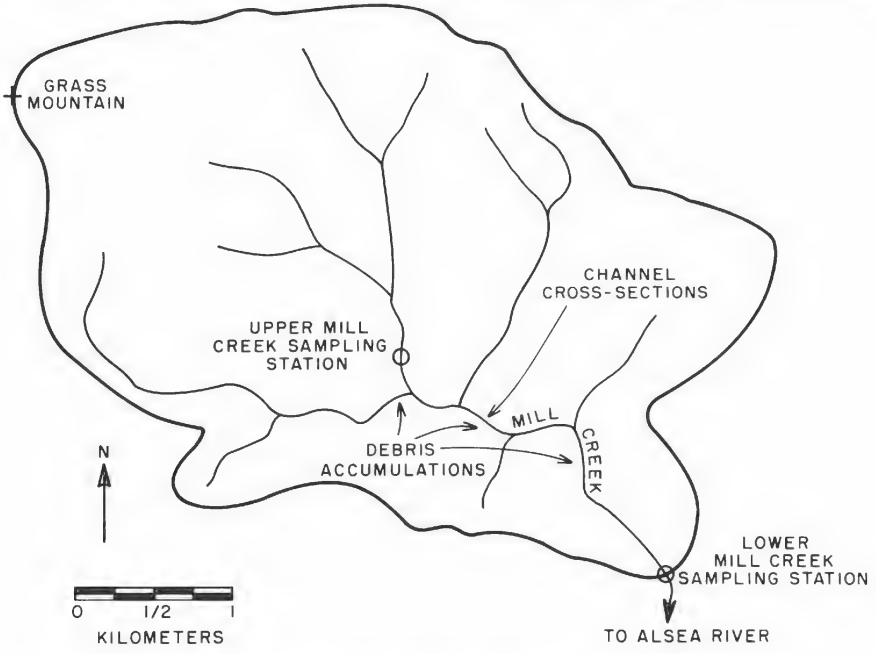

Figure 1. The Mill Creek drainage northeast of Alsea, Oregon.

as a third-order stream (Strahler, 1957)—has an average gradient of approximately 7 percent. The first- and second-order tributaries in this drainage have average gradients of 31 and 12 percent. Hill slopes adjacent to Mill Creek are steep and frequently exceed 75 percent. Elevations range from 150 m along the lower portion of Mill Creek to more than 1070 m on Grass Mountain.

Methods

The movement of sediment in Oregon's Coast Range streams depends on periods of storm activity and high flows. Although streamflow was not measured in Mill Creek, flow measurements for the North Fork of the Alsea River—draining 163 km^2 of watershed immediately north and east of Mill Creek—were used to index flow activity in the Mill Creek drainage.

Turbidity and suspended sediment concentrations were monitored above and below the debris removal sites (Fig. 1). The drainage areas above the upper and lower sampling station were 4.5 km^2 and 11.5 km^2, respectively. Sampler intakes, suspended in midstream at each location by cables anchored to the creek's banks, led to automatic pumps that collected one sample bottle every six hours. Each bottle contained a composite of four subsamples collected at 1.5-hour intervals. Sample bottles were collected weekly from 5 November 1975 to 24 March 1976 except for several periods when equipment malfunctioned. Turbidity, expressed as nephelometric turbidity units (ntu), was determined for all samples according to *Standard Methods* (American Public Health Association, 1971). Samples were filtered to measure the concentration of suspended sediments, expressed as milligrams per liter ($mg\ l^{-1}$).

To assess changes in channel characteristics, ten cross-sectional profiles were measured along a 100-m section of Mill Creek (Fig. 1) that had been cleaned by tractor operations. This section of Mill Creek was characterized by gravel-size sediments (approximately 2-64 mm in diameter) that had accumulated behind the debris obstructions. Cross-sectional profiles were first measured in September of 1975 after the debris removal operations of that summer. The transects were remeasured in July of 1976 after the 1975-76 winter runoff period.

Results and Discussion

From November 1975 through March 1976, daily stream flows on the North Fork (Fig. 2) approximated the average flow for the preceding 15 years (1962-76). Daily flows averaged 0.097 $m^3sec^{-1}km^{-2}$ or about 93 percent of the 15-year average for the November through March runoff period. A frequency analysis (partial duration series) of peak flows for the 15-year period indicated that the mean annual flood, with a recurrence interval of approximately 2.3 years, was 1.07 $m^3sec^{-1}km^{-2}$. During the 1975-76 winter runoff, discharge peaked at 1.02 $m^3sec^{-1}km^{-2}$ on 4 December 1975. Further comparison of flow duration curves indicated that the distribution of stream discharges during the five months resembled the average winter-flow distribution for the 15-year period. Thus, winter streamflow patterns, from November 1975 through March 1976, on the adjacent Mill Creek drainage probably typified nearly average conditions.

Upstream from the debris obstructions, substantial amounts of sediments had collected during the last 15 years. Removal of the large organic debris triggered localized scouring of sediment deposits. During summer and early fall of 1975, such channel

changes were relatively minor. However, immediately downstream from the original debris obstructions, several pools began to fill in with silt and sand-sized particles.

In general, most channel erosion was associated with the high runoff in mid-November and early December (Fig. 2). Downcutting continued until large rocks and cobbles were exposed. The effect of this channel scour and downcutting was apparent in the sediment loads measured at the two sampling stations (Fig. 3). Between 12-15 November and 3-5 December, turbidities at the upper station never exceeded 30 ntu, whereas turbidities at the lower station exceeded 100 ntu. This increase was caused by scouring of the sediment previously stored in the channel. Crews continued to remove organic debris by hand from Mill Creek throughout November and December.

Most of the channel downcutting had occurred by 1 January 1976. However, during the mid-January storms, turbidity increased at both the upper and lower sampling stations. Although both locations had turbidities far exceeding 100 ntu, turbidities at the upper station generally were double those of the lower station. This figure indicated that these sediments came from above the upper station and that the turbidity was diluted as the sediments continued downstream. For example, grab samples taken on 14 January 1976 indicated that several tributaries had turbidities of only 5 ntu, while the upper sampling station had turbidities exceeding 200 ntu. The mixing of turbid water from above the upper station (drainage area of 4.5 km^2) with relatively clear tributary waters between the two sampling stations (another 7.0 km^2 of drainage area) would

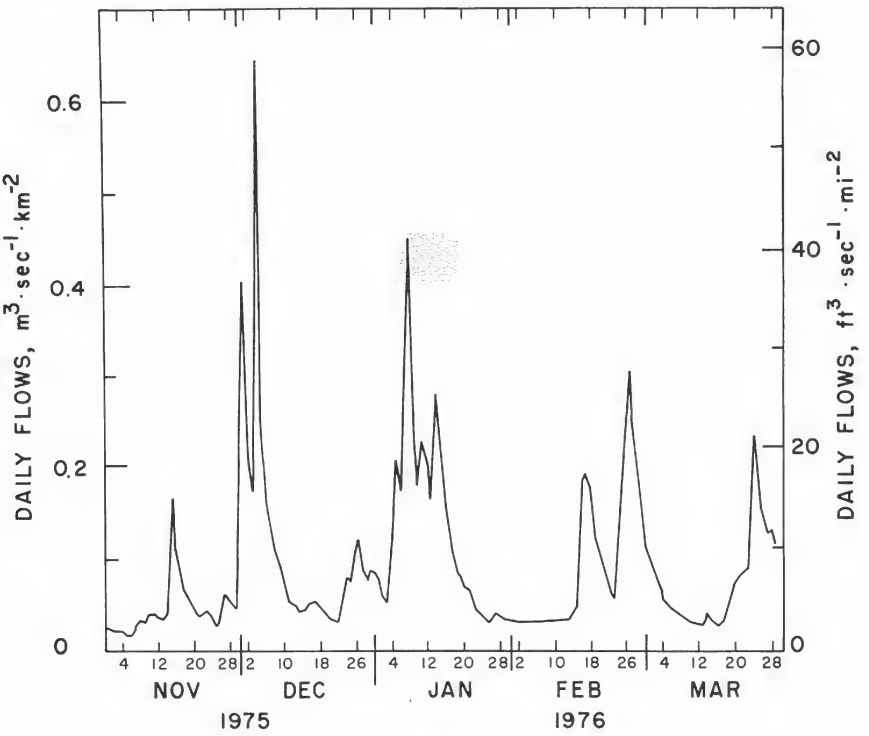

Figure 2. Streamflow for the North Fork of the Alsea River near Alsea, Oregon.

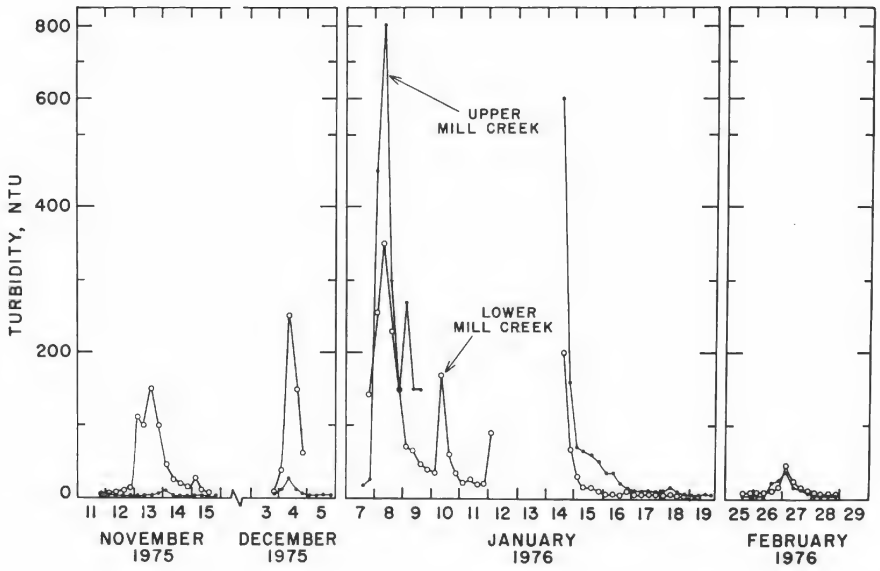

Figure 3. Stream turbidities in Mill Creek during periods of high runoff.

reduce downstream turbidities even though the total suspended sediment load remained relatively unchanged. Apparently that happened from 7-20 January 1976. Even if additional downcutting and scouring of sediments deposited behind the debris had occurred, the high turbidities originating above the upper station would have masked the effect on stream turbidities.

Following the high flows of mid-January, turbidity levels at both the upper and lower sampling stations responded similarly to subsequent storms and generally remained lower than those measured in mid-January. For example, although turbidities exceeded 200 ntu in the first half of January, subsequent turbidities at both the upper and lower sampling stations were always less than 200 ntu. During runoff from 25-29 February, turbidities at the upper and lower stations did not exceed 50 ntu (Fig. 3), indicating that the channel system had again started to stabilize. Throughout the winter, turbidity between periods of high flow generally remained below 10 ntu at both sampling stations.

Simple linear-regression analyses showed significant relationships (P=0.90) between turbidity and suspended sediment concentrations for both the upper and lower sampling stations. Because the two regressions did not differ significantly (Draper and Smith, 1966), the data from both stations were combined. The relationship between suspended sediment concentration (SSC) and turbidity (ntu) for Mill Creek is:

$$SSC=(2)(ntu)+55 \qquad r^2=0.77$$

Thus, changes in turbidity associated with periods of storm-generated streamflow and debris removal also reflected changes in the suspended sediment loads of Mill Creek.

Cross-sectional profiles confirmed that substantial channel scouring had occurred during the 1975-76 winter (Fig. 4). Along the 100 m reach where profiles were

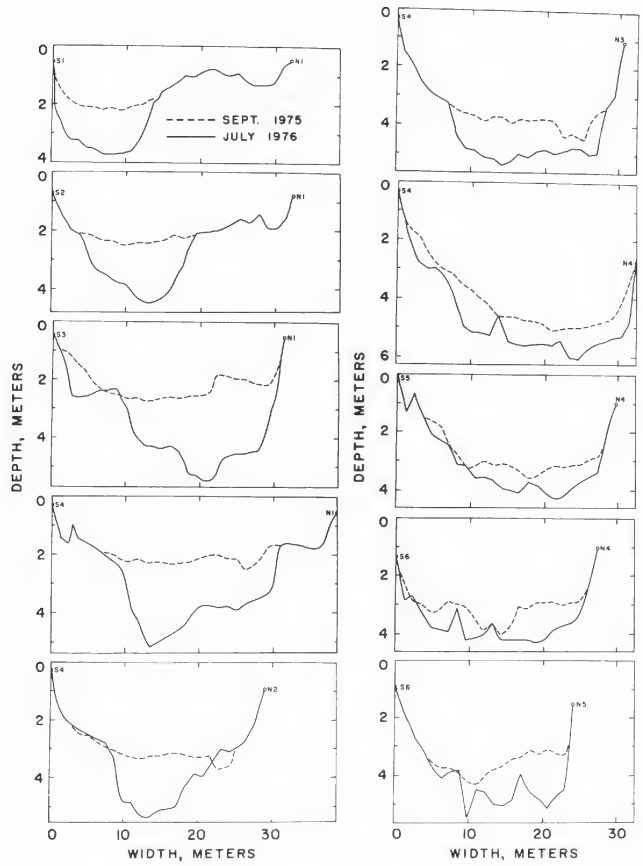

Figure 4. Cross-sectional profiles along a 100-m reach of Mill Creek stream channel. Cross-sections were spaced approximately 10 meters apart.

measured, Mill Creek underwent rapid downcutting. As a result, an average of 21 m^3 of sediment was removed for each meter of channel length. The depth of scour averaged 0.9 m, although maximum scour depths exceeded 2 m for one-half of the profiles. Assuming an average density of 1.8 t m^{-3} (Gottschalk, 1964) for water-deposited sediments, stream action removed nearly 3800 t of sediment along 100 m of channel. These values typified an additional 150 m of channel directly upstream from the cross-sections.

The bottom of the stream channel is now characterized by relatively coarse sediments (e.g., cobbles and boulders). Further downcutting probably will not occur, although lateral cutting from unstable banks on Mill Creek may cause additional sediment loading into the stream.

Summary and Conclusion

This study to quantify effects of debris removal on (A) stream turbidity and suspended sediment concentrations and (B) changes in channel geometry showed that:

(1) Turbidity provided an index of suspended sediment concentrations in Mill Creek;

(2) The greatest measurable increase in turbidity after debris removal occurred during the first several fall and winter storms;

(3) High flows in January were accompanied by high turbidities from upstream sources, thus masking any increases associated with the removal of debris;

(4) Relatively low turbidities occurred during late winter and spring storms, both above and below the debris removal section, possibly indicating that fines were quickly flushed from the watershed; and

(5) Downstream impacts should be considered in assessing trade-offs associated with debris removal and increased sedimentation. High flows during the 1975-76 winter significantly degraded sediments that had previously accumulated behind several of the debris dams. An estimated 5250 m^3 of sediment eroded from 250 m of channel, and the fate of this material is unknown.

A relatively large volume of sediment that had accumulated behind several debris dams during the previous 10 years was quickly eroded by fluvial action after the removal of large organic debris. Although the results represent a case study of one stream during one year, they nevertheless suggest what might be expected under similar conditions in other drainages of Oregon's Coast Range.

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Disturbance of Small Mammal Live Traps by Spotted Skunks[2]

Abstract

In 1975, during a study of the effects of controlled slash burning on small mammal communities in the Coast Range of western Oregon, traps were disturbed, and trapped animals experienced unusual predation. During mark-recapture trapping in October, 34 percent of the live traps were disturbed, and mice had been partially eaten in an additional 6 percent of the traps. Although some traps had been pulled to mountain beaver burrows, the capture of two spotted skunks (*Spilogale putorius*) in large traps at the site suggested that this species could have caused the disturbance and predation.

Introduction

Skunks occur throughout Oregon, particularly west of the foothills of the Cascade Mountains. Spotted skunks (*Spilogale putorius*) are important predators of small mammals (Bailey, 1936; Selko, 1937), further evidenced by mammal remains in scats of prairie spotted skunks (Crabb, 1941).

Disturbance of small mammal traps and unusual predation on the trapped animals occurred in 1975 during an investigation to study how controlled slash burning affected small mammal communities in the Coast Range of western Oregon. Ground squirrels (chiefly *Spermophilus beecheyi*) and other animals commonly disturb traps, and weasels (*Mustela* sp.) kill and infrequently eat trapped mice. However, we never observed traps disturbed in this way during similar studies, and evidence suggested that spotted skunks may have caused the disturbance.

Methods and Materials

Logged in 1955, the study area (56 km west of Corvallis at T 11 S, R 9 W, S5, Willamette Meridian) had reverted to a brushfield. Red alder (*Alnus rubra* Bong.), cascara (*Rhamnus purshiana* DC.), and Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] became the dominant overstory species, with a dense understory composed mainly of salmonberry (*Rubus spectabilis* Pursh), vine maple (*Acer circinatum* Pursh), and swordfern [*Polystichum munitum* (Kaulf.) Presl.].

To live trap small mammals, we located circular trap lines about 100 m in diameter on treated (burned) and adjacent untreated areas. Each line consisted of 40 stations

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spaced 8 m apart with two Sherman type live traps (8 x 9 x 25 cm) at each station. In addition, a welded wire live trap (23 x 23 x 80 cm) was placed at every other station. Bait was a mixture of whole rolled oats and Douglas-fir seed in the small traps and apples in the larger traps. Censuses of the small mammal populations were taken by removal trapping in June, then by mark-and-recapture trapping for three days in each of four periods—two in August (before and after burning), and one each in September and October.

During removal trapping on the untreated area, we captured 154 small mammals of 11 species, primarily *Peromyscus maniculatus* (55 percent), *Sorex* sp. (20 percent), *Microtus oregoni* (10 percent), and *Eutamias townsendii* (8 percent). Although mountain beavers were abundant, none was caught.

On the untreated area, one trap was sprung at each of two stations during the first trapping period in August and at each of eight stations during the second period. In September, 28 traps were disturbed at 20 stations (both traps at eight consecutive stations).

On 28 October, 11 traps at 8 stations were sprung, and 16 traps with *Peromyscus*, one with *Eutamias*, and one with *Microtus* were disturbed. The small mammals in these traps either were caught in the doors or their partially eaten remains were found inside the traps. On 29 October, 28 traps at 18 stations were sprung, and 11 of those traps had been pulled from 1-3 m to mountain beaver burrows. To determine what predators might be attacking the trap line, we baited the welded wire traps with mice. On 30 October, 27 traps at 22 stations were sprung, and 11 other traps held mice that had been killed and partially eaten. In addition, we caught two spotted skunks.

On the treated area, no traps were disturbed and no skunks were caught during these sampling periods, although small mammals were abundant before and after burning.

Discussion

Apparently, small mammal traps on the untreated area were disturbed in October 1975 by determined predators that had learned how to open the trap door and prey upon the trapped animals; yet these predators were large enough to avoid being captured themselves. Kale (1969) reported similar disturbance of small mammal traps. After 45-65 percent of 288 traps had been disturbed in four nights, he caught eight spotted skunks in larger traps set between trapping stations. Myton (1971) captured three striped skunks (*Mephitis mephitis*) in large live traps set after small mammal traps were repeatedly disturbed.

Pfeiffer (1953) caught 13 other mammalian species in unbaited steel traps set for mountain beavers, and 9 of the 36 animals caught were spotted skunks. Spotted skunks frequent the runways of mountain beaver, and Lovejoy (1972) reported spotted skunks as the most common burrow associate of mountain beavers. In this study, the transfer of 11 traps to the runways of mountain beaver burrows incriminates spotted skunks as the predators. During other studies, we occasionally caught both spotted and striped skunks in welded wire traps baited with apples and set in sites that ranged from recent clearcuttings to mature coniferous stands. In one unusual night we caught five spotted skunks in a group of 20 traps set in burrows to catch mountain beavers. Con-

sidering the two spotted skunks caught in our larger traps during this study, we believe that those animals were the predators disturbing our traps.

Thirty-four percent of the traps were disturbed each of the three trap nights in October. In addition, 6 percent more of the traps had small mammals that were partially eaten. The data from many trapped animals were lost to the predators.

By disturbing traps and preying on trapped animals, spotted skunks may cause unexpected interference with small mammal studies. Such disturbances may be avoided by using a device that will prevent the spotted skunks from getting access to the small mammal traps (Getz and Batzli, 1973).

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Population Analysis of the Mountain Beaver, Aplodontia rufa pacifica, in Western Oregon [2]

Abstract

A rotational system of live-trapping Pacific mountain beaver (*Aplodontia rufa pacifica*) on a weekly basis was conducted on a 5.5-ha (13.5-a) grid from July 1965 to August 1967. A total of 5144 trap nights over an 88-week period resulted in a catch of 181 mountain beavers. Of this total, 109 were adults and 72 were juveniles; males outnumbered females by a ratio of 1.62:1. The sex ratio of juveniles was 1:1. Population estimates on the grid ranged from a low of 41 in November to a high of 54 in July of the same year. Transients made up a large part of the catch. Conservative estimates of density on the grid plus a boundary strip of 40 m (131 ft) ranged from 4.2 to 5.4 animals per ha (1.7 to 2.2 per a). Survival rate of animals tagged in August 1965 was 64 percent after one year. Eleven of the 45 animals, or 24 percent, were still alive after two years. Some of the animals were sexually mature (2 years old or older) when first captured and were at least 4½ years old when last taken in 1967.

Introduction

We studied a population of Pacific mountain beavers (*Aplodontia rufa pacifica*) in the Coast Range of western Oregon from July 1965 to August 1967. The Pacific mountain beaver, one of seven subspecies of *Aplondontia* (Dalquest and Scheffer, 1945), occurs principally in the Coast Range and interior valleys of western Oregon. In this paper, we summarize the results of our analyses of population structure.

Study Area

The study area, located in Section 8, T12S, R7W in Benton County, Oregon, has an elevation between 488 and 518 m (1600 and 1700 ft) and a mild climate of wet winters and dry summers. The vegetation was in a seral stage after logging and partial slash burning in the 1940s. The site was occupied by young-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and red alder (*Alnus rubra* Bong.). The shrub layer was irregularly distributed and poorly developed over most of the area. Herbaceous vegetation, which attained maximum development and matured during July, was dominated by bracken fern (*Pteridium aquili-*

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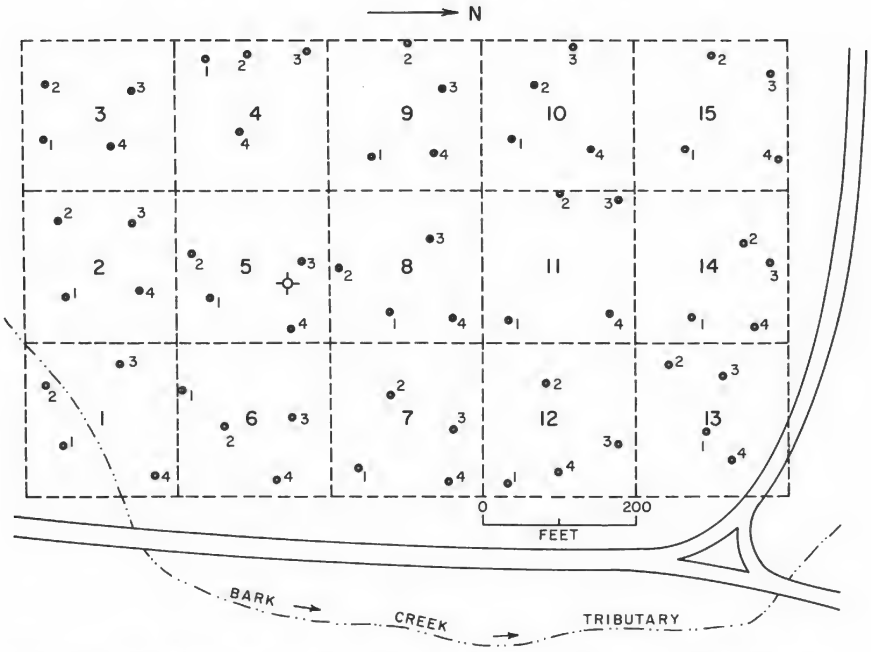

Figure 1. Trapping grid on the study area. The grid enclosed 5.5 ha (13.5 a) and was subdivided into 15 blocks, each containing four trapping stations.

num (L.) Kuhn). This fern and western sword fern (*Polystichum munitum* (Kaulf.) Presl) provided an abundant food supply for the mountain beavers during much of the year.

Methods

A rectangular trapping grid (Fig. 1), 302 by 181 m (990 by 594 ft) and enclosing 5.5 ha (13.5 a), was located on a gentle east-facing slope, bounded by moderate north- and south-facing slopes. We live-trapped for one night each week (with some exceptions) and moved traps weekly, a method based on procedures devised by Brant (1962). During August 1966, we trapped the area adjacent to the grid boundary. Mountain beavers were captured in live traps, 15 x 15 x 61 cm (6 x 6 x 24 in), which were baited with apples and set in burrows or runways. Captured animals were transferred from the traps to a handling cage (Black and Hooven, 1972) for marking with eartags, examination, and measurement. Animals were sexed and aged according to three age classes (juveniles, yearlings, and adults), based on size and weight, pelage, and reproductive condition.

We followed a method of "direct enumeration" (Fleming, 1971) in studying monthly population sizes. Table 1 shows how monthly population size was estimated. Column A lists the number of animals captured each month on the grid. Column B includes animals captured before and after but not during that particular month. These animals were assumed to have been a part of the population during the intervening

period. The estimated size of monthly populations, column C, consists of the sum of columns A and B.

TABLE 1. Estimates of population sizes and densities.

Date	Monthly captures A	Skipped captures[a] B	Population size C	Density Per acre[b] D	Per ha
1965					
September	32	21	53	2.1	5.3
October	26	23	49	2.0	4.9
November	36	14	50	2.0	5.0
December	26	25	51	2.1	5.1
1966					
January	24	29	53	2.1	5.3
February	25	28	53	2.1	5.3
March	15	34	49	2.0	4.9
April	20	27	47	1.9	4.7
May	29	16	45	1.8	4.5
June	39	12	51	2.1	5.1
July	44	10	54	2.2	5.4
August	36	16	52	2.1	5.2
September	34	16	50	2.0	5.0
October	18	25	43	1.7	4.3
November	25	16	41	1.7	4.1
December	21	20	41	1.7	4.1
1967					
June	25	17	42	1.7	4.2
July	39	6	45	1.8	4.5
Average	28.55	19.72	48.27	2.0	4.8

[a]Captures of tagged animals made before and after that particular month.

[b]Densities based on an estimated effectively trapped area of 10.0 ha (24.6 a).

Population estimates based on direct enumeration were compared with estimates based on the Lincoln Index.

In calculating population densities, we added to the grid of 5.5 ha (13.5 a) a boundary strip of 40 m (131 ft), equal to the average distance (avg D) between successive captures of adults. This addition gave 10.0 ha (24.6 a) as the estimated size of the area effectively trapped. Brant (1962) showed that avg D is a function of the movement patterns of the species trapped and that the actual area trapped should include the strip surrounding the grid of width equal to avg D.

Results and Discussion

Trapping Results

A total of 5144 trap nights (4784 on grid and 360 off grid) over an 88-week period resulted in a catch of 181 mountain beavers. Availability of food and cover, behavioral differences between sexes and between juveniles and adults, and weather affected trapping success, which averaged 17 animals per 100 trap nights. Of the 181 animals trapped, 109 were adults and 72 were juveniles; males outnumbered females by a ratio of 1.62:1. The sex ratio of juveniles was 1:1. Of the 150 mountain beavers taken on the grid, 26 were captured 10 or more times. However, 44 (27.8 percent) of the animals tagged and released on the grid were never retrapped. Trapping mortalities represented a significant loss to the population. Of 181 animals captured, 18 died in traps.

Estimation of Population Numbers

Problems are encountered in using recapture data to estimate population sizes and densities (Dunnet, 1964). Most methods for estimating population size and density of small mammals require that the population is sampled randomly, that all animals have an equal chance of being caught, and that the population is not altered significantly by recruitment or emigration during the study.

Although we cannot verify all of these assumptions, we found no marked differences in trap responses between the sexes, as indicated by the frequency of recapture of marked animals. Possibly marked animals entered traps more readily than unmarked animals, or individuals with more trap experience were caught at a faster rate than those with less experience (Fleming, 1971). A few animals were captured often enough to suggest some trap proneness, but we believed that the rotational system of moving the traps weekly alleviated this tendency.

Fleming (1971) considered that nonrandom sampling was the most serious violation of the assumptions in population estimates. He found that his marked animals (tropical rodents) were caught at a faster rate than unmarked animals. To avoid using conventional methods based on assumptions known to be violated, Fleming relied on "direct enumeration" to determine monthly population sizes. Similar techniques were followed by Dunnet (1964) in his study of the brushtailed possum in Australia and by Tamarin and Malecha (1971) in a study of two species of rats in Hawaii.

An inherent weakness of this method is the assumption that animals occasionally caught were present continuously between captures, which causes difficulty in dis-

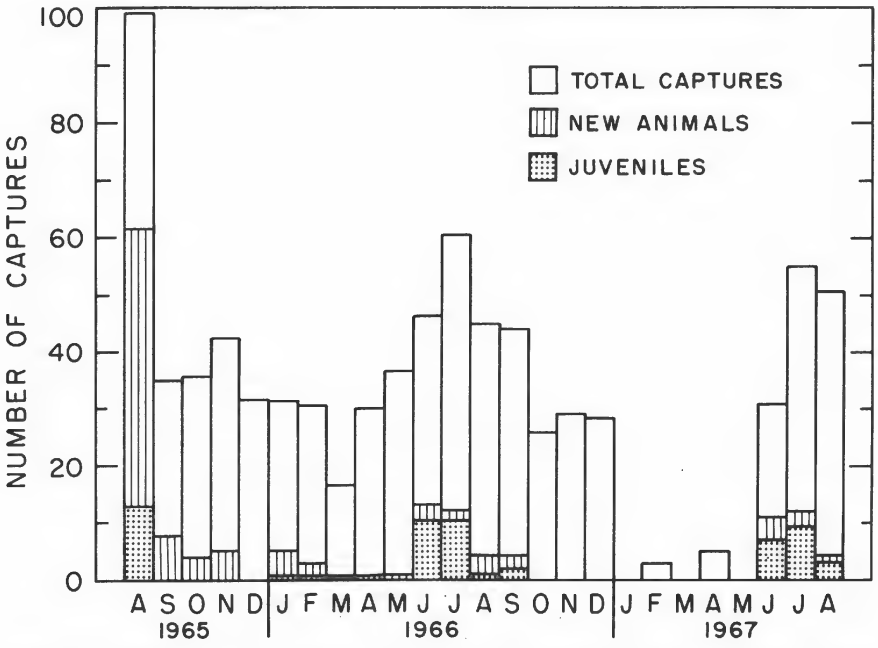

Figure 2. Monthly capture record of animals taken during weekly trapping, which was discontinued from January through May 1967.

tinguishing between resident and transient animals. The possibility also exists that some individuals may never be captured. Because we were dealing with a population in which a large percentage was marked (Fig. 2), this technique of handling recapture data seemed likely to produce reliable estimates.

Population Estimates

Population numbers on the grid ranged from a low of 41 during November and December 1966 to a high of 54 in July of the same year. A gradual decline during the spring of 1966 was followed by a sharp upswing in June and July because of the recruitment of young animals into the population. The high population estimates for January and February of 1966 resulted from the large numbers of uncaught animals known to be there.

The population showed a decline in the second year of the study, which may reflect the adverse influence that trapping had on the population.

The highest number of monthly captures, 44 (Table 1, Column A), also occurred during July. The lowest number of captures, 15 (only four were females), occurred in March. These differences reflect the fluctuations in trapping success, which were highest in summer and lowest in winter. Poor success in trapping coincided with the reproductive season, but the catch improved rapidly after parturition in April.

Population Densities

Density estimates depend on knowing the number of animals in a population and the size of the area occupied. Accurate estimates of both these unknowns are difficult to obtain. Brant (1962) pointed out that ". . . wherever the habitat is relatively continuous, density estimates must take into account the distances that animals have come to traps."

In determining the effectively trapped area, some workers have added to the grid size a boundary strip equal to half the average distance of movement (Stinson, 1964), or half the width of the average home range (Blair, 1941; Jones and Barber, 1957). Others have used a strip equal in width to the average distance between successive captures (Brant, 1962; Lidicker, 1966; Fleming, 1971).

Addition of a boundary strip of avg D probably overestimates the size of the area effectively trapped in our study for several reasons. The habitat was not occupied uniformly by mountain beavers around the perimeter of the grid. Blocks 9 and 10 on the west side of the grid were not trapped regularly because of this fact, and blocks 8 and 11 contained few active burrows. Avg D for the population also may have been overestimated because about two-thirds of the adults caught were males, and data were based on twice as many males as females. Avg D for adult males, 44 m (144 ft), was significantly larger than for adult females, 32 m (105 ft) ($P<0.05$). Also, avg D for juveniles, 33 m (107 ft), was smaller than for adults, 40 m (131 ft), although the difference was not significant ($P<0.05$). Furthermore, no tagged animal from the grid ever was captured farther than 18 m (60 ft) from the grid boundary. Conversely, no animal taken farther than 18 m (60 ft) from the boundary during trapping of the peripheral area was ever retrapped on the grid.

The density estimates ranged from a minimum of 4.2 animals per ha (1.7 per a) to a maximum of 5.4 per ha (2.2 per a). Because these densities are calculated on the basis of the entire grid area, plus the boundary strip, they probably are conservative.

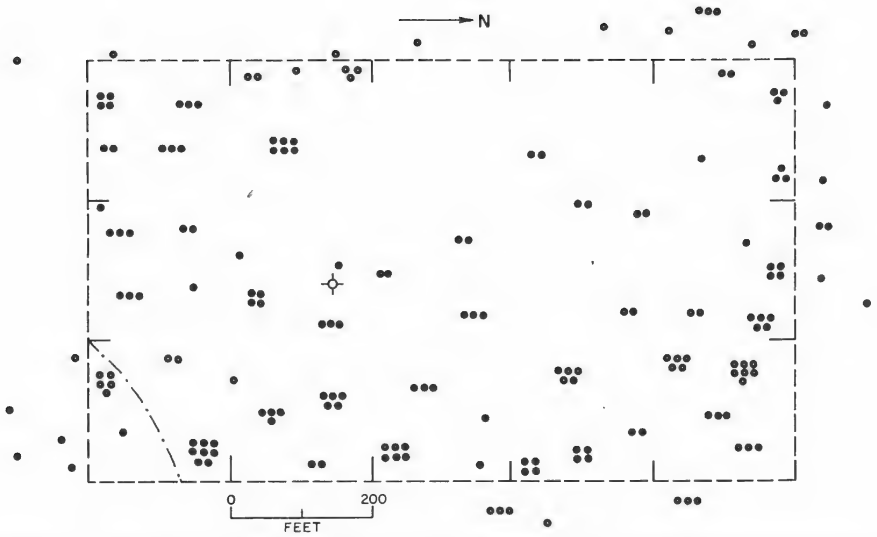

Figure 3. Distribution of captures of 181 mountain beavers on the study area. Only the site of first capture is shown for animals caught more than once.

Moreover, the density of occupied areas was considerably greater than the estimates for the entire grid would indicate (Fig. 3).

As a comparison, we applied the Lincoln Index to estimate the population at the beginning of the study. With the number of animals originally tagged and released in August (57), the total number captured in September (32), and the number of recaptures in this second sample (24), the equation is:

$$N = Mn/m, \text{ or } N = (57)(32)/24.$$

The population (N) equaled 76 ± 7.8, or 7.6 animals per ha (3.1 per a). This figure suggests that the direct-enumeration method may have underestimated the population. At the 95 percent confidence level, however, the population lay between 60.5 and 91.5 animals. This lower limit is comparable to the monthly estimates obtained by direct enumeration (Table 1).

During the first month of trapping, 62 new animals were captured on the grid. Fourteen of these were single captures that were never seen again. If only half of those 14 were considered transients, that indicates a population of 55 animals.

During the first four months of trapping, 79 different animals were captured. For five weeks after the capture of the last new animal, no new animals were taken. If the 20 single captures and the seven trap mortalities that occurred during this period are deducted from the cumulative total, the population for January is 52 animals. This compares closely with the estimated population of 53 for January (Table 1).

Throughout this study, the biomass (wet weight) of *Aplodontia* varied from 3.4 to 4.5 kg per ha (3 to 4 lbs per a).

Few data exist on population estimates of mountain beavers. Camp (1918) reported trapping 11 specimens from an area 152 x 30 m (500 x 100 ft) on which he counted 100 burrow entrances. Voth (1968) removed 21 animals from 2 ha (about 5 a) near

our study area during the spring, summer, and fall of 1964. In both instances, if a boundary strip of the same width as we used (40 m) [131 ft] were added, the population density would have been the same, 4.2 animals per ha (1.7 per a), and identical with our minimum estimate.

Survival and Longevity

Of the 45 animals tagged and released in August 1965 and recaptured later, at least 29 were known to be alive one year later. This is a survival rate of 64 percent. Eleven of those 45 animals, or 24 percent, were still alive two years later.

Some of the animals captured in 1965 that were sexually mature (two years old or older) were at least four years old when last captured in 1967. Based on these data, we estimate that life spans of five to six years are not uncommon for the mountain beaver.

Martin (1971) monitored two radio-tagged adult mountain beavers for 31 and 44 months. He estimated that these animals would have been about five and six years old if they had been two years old when tagged.

Sex Ratios

Few data have been published on the sex and age ratios of mountain beavers. Hubbard (1922) reported that 75 percent of the animals he trapped on the University of Washington campus were males. Voth (1968) was unable to distinguish between the sexes of immature animals, but among the 22 adult animals trapped, he reported that 63.6 percent were males. This figure is comparable to the results of our study.

Of the 181 animals trapped, males outnumbered females 112 to 69. This was a ratio of 1.62:1, or 61.9 percent males. Considering only the 158 animals trapped on the grid, the ratio was 1.59:1, or 61.4 percent males. Although the sex ratio among wild juveniles varied from year to year, the ratio of 72 young *Aplodontia* from three successive breeding seasons was exactly 1:1.

The numbers and sex ratios of juvenile and adult animals captured on the grid are summarized in Table 2.

TABLE 2. Numbers and sex ratios of juvenile and adult mountain beavers caught on the grid each year from 1965 to 1967.

	Juveniles				Adults[a]			
Year	Males	Females	Total	Percent Males	Males	Females	Total	Percent Males
1965	9	7	16	56.3	48	18	66	72.7
1966	14	13	27	51.9	48	27	75	64.0
1967	8	11	19	42.1	22	11	33	66.7
Totals	31	31	62	50.0	118	56	174	67.8

[a]Adult figures for 1966 and 1967 include yearling animals.

Deviant sex ratios in favor of males in wild populations are usually attributed to behavioral differences in response to trapping. The causes of these differences most commonly cited are that males are more active and range more widely, which increases their probability of capture over the females. We interpret the preponderance of males, however, as an actual numerical superiority, and the sex ratio of adults appears to be a true ratio and not an artifact of trapping.

Age Structure

Pfeiffer (1958) recognized four classes based on the degree of closure of the epiphyseal femoral suture and tooth wear. Voth (1968) established eight age classes, which included five for adults, based on minor differences in weight. This categorization would appear inadvisable because of the great variation possible within individuals and the extent of overlap in the weights of juveniles with adults. Some juveniles at five months weighed more than some small adults (Lovejoy and Black, 1974).

Although we were able to recognize three age groups based on external characteristics, some late yearlings could not be distinguished from adult animals. The age composition of the grid population for 1966 is shown in Table 3.

TABLE 3. Age composition of the grid population during 1966.

	Juveniles	Yearlings[a]	Adults	Totals
Males	14	4	44	62
Females	13	2	25	40
Totals	27	6	69	102

[a]Yearling class consisted of known juveniles from the previous year.

Of the 181 mountain beavers captured, 72 were juveniles and 109 were adults, yearlings included, a ratio of 1:1.51: 60.2 percent were adults.

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Battery-Light Tracking as a Technique for Studying Small Nocturnal Mammal Movements

Abstract

Movements of small nocturnal mammals may be monitored by attaching a small battery-light packet to individuals. Detected movements may be plotted in relation to a lighted grid or prominent physical features. The technique provides specific data concerning home range and microhabitat utilization in terms of temporal, spatial, and physical relationships.

Accurate data on movements of small nocturnal mammals are difficult to obtain. The majority of data have been collected by trap-mark-recapture methods, a technique with several limitations (Sanderson, 1966). In addition to having several inherent sources of error, trapping yields few data concerning the manner in which animals actually use the area defined as home range. In reviewing movements of small mammals, both Jewell (1966) and Sanderson (1966) have stressed the need for more information on activities and behavior within what is normally defined as home range. Attempts to provide more accurate data on both size and utilization of home range by using alternative techniques such as radioisotope tagging (see Ambrose, 1960; Godfrey, 1953), paper tracking (Sheppe, 1965; Justice, 1961), sand tracking (e.g., Siniff and Tester, 1965) have met with varying degrees of success. In a recent article, Buchler (1976) suggested the use of a chemiluminescent tag for tracking small nocturnal rodents. The merits of the technique were enumerated and details of procedure given. Also included was a brief reference to the related technique of marking with miniature light bulbs used in combination with small mercury batteries. The purpose of the present paper is to report on the detailed use of this latter technique which we have employed in the tracking of small mammals for several years.

Basically, the technique consists of attaching a "sub-miniature" light and a small mercury battery to an animal so that it may be followed visually at night. This technique is a modification of one used by Bellrose (1958) for tracking wild mallards at night. Additional lights, color coated mount-type pinlights attached to D-cells, are used to mark a grid or identify prominent landmarks so that movement distances of the experimental animals are more easily ascertained. This basic technique has been used on five species of small rodents and some other nocturnal animals with generally good results.

Figure 1. Adult *Peromyscus truei* with battery-light packet attached.

Several combinations of batteries and lights have been tried. The best combination found to date is a size 675 mercury battery and a JKL Components Corporation (2226 Barry Ave., West Los Angeles, CA 90064) WL1516 lamp having a life of approximately 16 hours. The 675 cells may be purchased as a number 177 battery which is a series of 675 cells connected by metal bands. When cut, the bands become tabs which may be used, after notching, as convenient connection points for the lamp leads without soldering. The light from this combination may be seen on a dark night up to 260 m with unaided vision. The battery-lamp pack, which weighs less than 2.5 gm, is attached to the animal by gluing it to the fur (Fig. 1), most successfully on the head between the ears, using Goodyear Pliobond Cement or Weldwood Contact Cement. Mice seem to carry the pack in this fashion without visible impairment of movement or activity. If the battery has a small piece of plastic electrician's tape glued to the base before attachment, it facilitates later removal by allowing separation of the battery from the tape rather than from the fur.

Connection of the lamp to the battery leads and attachment to the animal may be done in the field immediately after capture or in the lab with an animal held over from the previous night's trapping. There are some drawbacks to both methods, but current data from tracking *Peromyscus truei* indicate that apparently normal activity is resumed after animals are held over for a day before tracking. Ideally, the best results might be obtained if an animal were instrumented and tracked immediately after being trapped. This procedure is usually not possible without a trap signal to show when a trap has been entered. The alternative method of frequently checking traps, however, may influence normal activity patterns and trap success. Morning trap check and hold-over has the advantage of providing a larger number of individuals from which to select an experimental animal.

The data obtained by visual observation may be plotted in the field by recording the position of an instrumented animal in relation to the light grid pattern, or outstanding landmarks. A continuous line, with time of observation marked periodically, similar to the technique employed by Siniff and Tester (1965) for plotting some radio telemetry data, has been used successfully. Data plotted in this manner give a good representation of both the temporal and spatial utilization of home range. It represents a refinement of movement data obtained by traditional trapping methods with the added benefit of providing information on specific movement responses to both natural obstacles, such as rocks, vegetation, and waterways, and changing environmental conditions such as wind, rain, moonlight, and cloudcover. The technique also provides a relatively inexpensive and rapid means of locating homesites, important for many kinds of field studies.

Figure 2 is an example of how data collected in this manner may be plotted for interpretation or presentation. The figure shows data for *Peromyscus crinitus*, obtained near Diamond Craters, Harney County, Oregon, on the east edge of Malheur Wildlife Refuge. Several mice were light tracked by Fisher during July, 1975. By plotting the data in relation to a photograph of the habitat, several aspects of behavioral ecology may be noted. In addition to ascertaining overall range and duration of movements

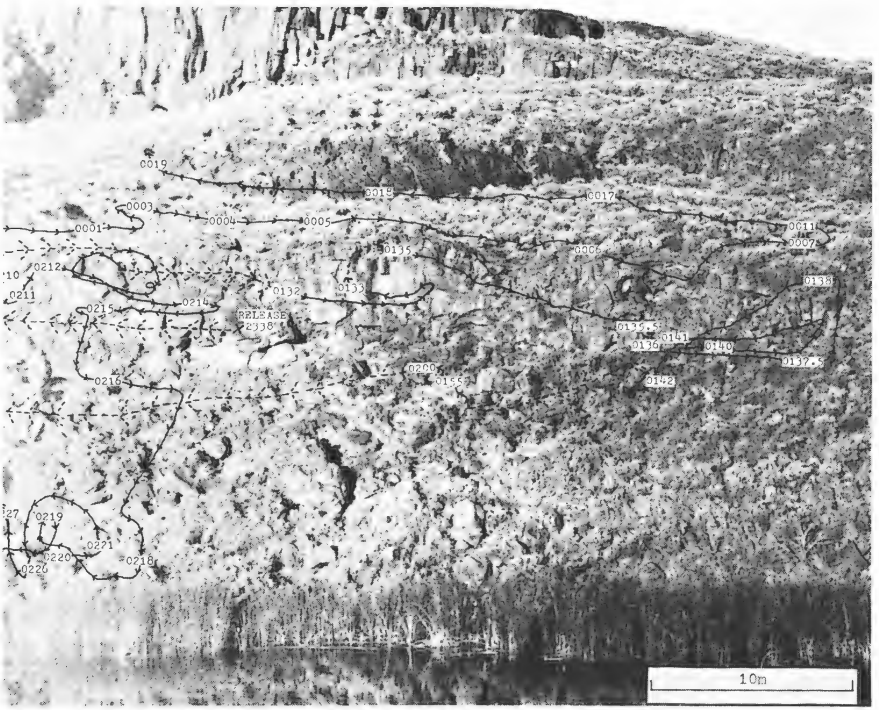

Figure 2. Part of one night's tracking data for a sub-adult male *Peromyscus crinitus*, obtained 14 July 1975, superimposed on a photograph of the corresponding part of the habitat. Location: Diamond Craters, Harney County, Oregon. Numbers=time of observation; solid lines=animal visible; dotted lines=animal not visible.

accurately, the relation to habitat is readily apparent. Referring to the specific case in point, one can deduce that the study animal traveled as fast at 27.3 m per minute between 0135 and 0135.5. More importantly, one can see that virtually all activity was confined to the rocky substrate whereas patches of bare ground and highly vegetated areas were avoided. Extended observations of this type allow precise examination and description of micro-habitat selection, utilization, and dimensions. Trapp (1972) used a generally similar technique for gathering behavioral data on ringtails, *Bassariscus astutus*, in the wild. The data may be treated quantitatively in a manner similar to that used by M'Closkey (1975) in his description of habitat for *Peromyscus leucopus*. Moreover, the observations confirm habitat affinities deduced from trapping studies (Deacon, *et al.*, 1964; Egoscue, 1964).

The technique has been tested, to varying degrees, on five species of nocturnal rodents, *Dipodomys heermani*, *Dipodomys ordi*, *Neotoma fuscipes*, *Peromyscus crinitus*, and *Peromyscus truei*. Cross has also used the technique for tracking homing bats, *Pipistrellus hesperus* and *Antrozous pallidus*. The battery-light package, modified by waterproofing in silicone rubber, has also been used to study the nocturnal movements of the Pacific pond turtle, *Clemmys marmorata*. Although the argument may be made that the weight and light of the tracking device affect the normal behavior of the instrumented animal, experiments with the above mentioned animals show that some aspects of nocturnal movements are more accurately ascertained in this manner than by any other known technique.

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Occurrence of 0-age English Sole, Parophrys vetulus, along the Oregon Coast: An Open Coast Nursery Area?

Abstract

Estuaries are known to be important as nursery areas for English sole, *Parophrys vetulus*, during a portion of their first year of life. This study collected 0-age *P. vetulus* in the ocean off Moolach Beach, Oregon, during 1974. Seasonal occurrence, depth distribution, and length-frequency data for 719 *P. vetulus*, 23 to 324 mm long, collected at depths of 15 to 52 m are presented. We suggest that, in addition to estuaries, unprotected nearshore areas along the Oregon coast are used by 0-age *P. vetulus*. Low density or localized utilization of these areas could be an important factor determining total *P. vetulus* production off Oregon.

Prior to this paper, 0-age English sole, *Parophrys vetulus*, have been reported to occur in estuaries (Westrheim, 1955; Smith and Nitsos, 1969; Misitano, 1970; Olsen and Pratt, 1973; Pearcy and Myers, 1974) and shallow protected inland coastal areas (Ketchen, 1956; Kendall, 1966; Van Cleve and El-Sayed, 1969). Olsen and Pratt (1973) suggested that estuaries may be the exclusive nursery areas for English sole along the Oregon coast, based on the incidence of a parasite infestation thought only to be acquired in estuaries. This paper is the first documentation of 0-age *P. vetulus* occurrence in the ocean off Oregon. Data are presented on seasonality, depth distribution, and length frequencies of 719 *P. vetulus*, 23-324 mm long, collected at depths of 15-52 m off Moolach Beach, Oregon, during 1974.

Moolach Beach is approximately 6.7 km of unprotected sandy beach on the central Oregon coast between Yaquina Head, to the south, and Cape Foulweather, to the north. Yaquina Head and Cape Foulweather are rocky headlands which separate the area sampled from the nearest estuaries: Yaquina Bay, 10 km to the south, and Siletz Bay, 26 km to the north. All specimens were collected in a 4.88 m, headrope length, semi-balloon box trawl having 3.81 cm body mesh, 3.18 cm cod end, and 1.27 cm cod end liner mesh (stretched measurements). All trawls began at latitude 44°42.5′N and were made on a heading of 0° true at approximately 3.7 km h (2 knots). Tows were 10 minutes long, timed from trawl reaching bottom to beginning of retrieval. Three lines were sampled: Line A—beginning 1.2 km from shore, 15 m depth; Line B—beginning 2.4 km from shore, 27 m depth; and Line C—beginning 4.8 km from shore, 52 m depth. Samples were collected twice monthly between June and October, and once in February and November, 1974. All fish were preserved in the field with 10 percent formalin; in the laboratory they were transferred to 40 percent isopropanol, identified, and measured. Lengths reported are standard lengths measured to the nearest millimeter.

Total lengths of 719 *P. vetulus* were also measured and regressed on standard length

producing the equation [Y=0.57+1.19X where Y= total length in mm and X= standard length in mm (R=0.999)]. This equation was then used to convert total length measurements reported by other workers to standard length for comparative purposes. For the purpose of this paper, we assumed that all *P. vetulus* <117 mm were 0-age. This limit is somewhat arbitrary but is based on age-growth studies by Westrheim (1955), Kendall (1966), Smith and Nitsos (1969), Van Cleve and El-Sayed (1969), and Olsen and Pratt (1973). This limit probably does not include all 0-age fish taken.

Two distinct size groups of 0-age *P. vetulus* were collected from the study area throughout 1974 (Fig. 1). The smaller size group was composed of fish <80 mm; the larger size group was of 80-117 mm fish. The frequency of occurrence of each size group varied with water depth. *Parophrys vetulus* <80 mm were taken in every tow on Line A (15 m depth) between 3 June and 22 October 1974, except one tow made on 20 June. These small fish were the only size collected at this shallowest station, except for two specimens >250 mm taken in August. On Line B (27 m depth), *P. vetulus* <80 mm were the most regularly captured group, occurring most commonly during August and September. On 24 September no fish <80 mm were taken, but fish 80-117 mm were taken along with some larger fish. Only a few *P. vetulus* <80 mm were taken on Line C (52 m depth), and those were captured during October and November. Juveniles 80-117 mm were present on this line throughout the sampling period except on 5 November. Larger fish occurred on this line in relatively large numbers throughout the year.

The low numbers of 0-age English sole taken at our shallowest lines on 22 October and 5 November may indicate a fall movement offshore. Other workers (Westrheim,

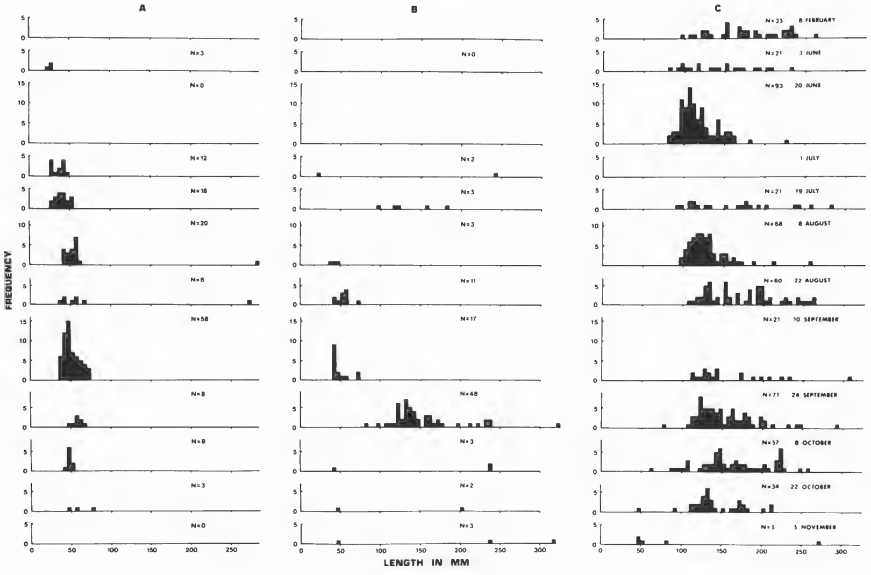

Figure 1. Length frequency of *Parophrys vetulus* captured on Line A=1.2 km (15 m depth), B=2.4 km (27m depth), and C=4.8 km (52 m depth) off Moolach Beach, Oregon, during 1974 (N=number of fish captured; when N is absent, sampling was not attempted).

1955; Olsen and Pratt, 1973) have reported fall emigration of juvenile *P. vetulus* from Yaquina Bay to offshore areas. The presence of two size groups of 0-age *P. vetulus* in our samples is probably a result of spawning peaks during the fall of 1973 and winter-spring of 1974. A detailed discussion of variations in time of English sole spawning is presented by Laroche and Richardson (in press).

Abundances of 0-age *P. vetulus* off Moolach Beach in 1974 appeared considerably lower than those found in Yaquina Bay by Westrheim (1955) and Olsen and Pratt (1973). However, comparisions were difficult to make due to differences in sampling gear, tow length, and tow speed. Ketchen (1956) took 0-age *P. vetulus* in greatest numbers from waters shallower than our shallowest line (15 m depth). This fact suggests that greater abundances may have existed in shallower waters adjacent to our study area.

There have been no adequate studies of juvenile flatfish occurrence in nearshore areas of the open coast off Oregon. The presence of 0-age *P. vetulus* in the study area off Moolach Beach suggests that at least some portion of this age-group may spend its first year in shallow open coastal areas instead of exclusively in estuaries as suggested by Olsen and Pratt (1973). Separation of the study area from the relatively distant estuaries by rocky headlands makes it unlikely that the 0-age specimens collected were actively moving to or from an estuary.

Considering the vast amount of shallow, sand bottomed, unprotected nearshore area and relatively small estuarine area along the Oregon coast, it seems possible that even low density or localized utilization of this area by 0-age *Parophrys* could be an important factor determining total *P. vetulus* production within Oregon waters.

Acknowledgments

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Response of Small Mammals to Herbicide-Induced Habitat Changes[2]

Abstract

Halves of three clearcuttings in western Oregon were treated in the springs of 1970 and 1971 with a combination of herbicides, principally atrazine and 2,4-D, to control herbaceous vegetation. Vegetation and small mammal communities were sampled before and after herbicide applications on both treated and untreated areas. Herbicide treatments reduced the number of plant species, chiefly grasses and forbs, and ground cover. However, survival and growth of Douglas-fir *(Pseudotsuga menziesii)* and growth of most shrubs were greater on treated areas.

Microtus oregoni, Peromyscus maniculatus, Sorex vagrans, Sorex trowbridgii, and *Zapus trinotatus*—comprising 95 percent of the total small mammal community—were abundant enough for meaningful evaluation. Mark-recapture data showed that the kinds and numbers of small mammals were similar between the sides of each designated area before treatment. However, effective control of herbaceous vegetation altered the species composition of small mammal communities as they responded according to their habitat preferences. Species preferring grassy habitats were less abundant on treated than untreated plots.

Introduction

Proper application of herbicides at recommended rates poses little danger to wildlife yet controls vegetation that competes with conifer seedlings for moisture, light, nutrients, and space (George, 1961; Brown, 1967). Few studies, however, report the effects of herbicide-induced habitat changes though they may affect the impact of animal damage on forest regeneration (Lawrence, 1967).

This paper reports responses of small mammals to herbicide-induced changes in habitat by examining changes in vegetation and how those changes affect the size and composition of small mammal communities.

This study was supported in part by a grant from the Bureau of Land Management, Department of the Interior. Responses of black-tailed deer to habitat change after herbicide treatment were reported separately (Borrecco *et al.*, 1972).

Study Area

In western Oregon, we studied three clearcuttings—at Carlson Creek and Williams Creek near Cottage Grove and at Maxfield Creek near Corvallis—that were similar in age, past treatment, stocking, cover, wildlife use, and physiographic features.

All three areas, lying in the *Tsuga heterophylla* zone (Franklin and Dyrness, 1960),

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were administered by the Bureau of Land Management. These large clearcuttings, 12-28 ha (30-70 acres), had been logged and burned 8 to 12 years before the study. The three sites were in the late weed stage of secondary succession, but approaching a shrub-dominated period. All had uniform cover, gentle topography, southern exposure, and heavy deer usage. As repeated attempts to reforest these areas had failed because of vegetative competition and animal damage, herbicide treatment was planned to facilitate forest regeneration.

The climate for all three areas is characterized by mild wet winters, dry summers, small diurnal variations in temperature, and prolonged cloudiness. Most precipitation falls as rain between October and March (Franklin and Dyrness, 1969).

Herbicide Treatments

Before bud burst in the springs of 1970 and 1971, helicopters sprayed half of each study area with a combination of herbicides designed to control grasses and forbs without injuring Douglas-fir *(Pseudotsuga menziesii)*.

A combination of 1.8 kg (4 lb.) each of atrazine and dalapon and 0.5 kg (1 lb.) each of 2,4-D and silvex in 76 l (20 gal.) of water was applied to each 0.4 ha (1 a) treated in the first year. To control shrubs more effectively, the mixture was modified in the second year to 1.8 kg (4 lb.) each of atrazine and 2,4-D in 68 l (18 gal.) of water and 6.6 l (2 gal.) of diesel oil per 0.4 ha (1 a). Dalapon was eliminated because perennial grasses were less abundant.

Sampling Methods

Vegetative Sampling

A reconnaissance survey before application of herbicides showed that the areas were uniform in vegetative cover and species composition.

We established sampling grids of 40 stations spaced at intervals of 30.5 m (100 ft) on each of the six plots (one grid on each half of the three test areas). A circular subplot of 0.0004 ha (1 mil-acre) centered at each station was the sampling unit. We recorded all plant species rooted within 10 sampling units randomly selected from the 40 stations on each plot, and we estimated the frequency of occurrence for each species by calculating the percentage of subplots in which it was found. Cover class values for grasses, forbs, and shrubs also were estimated (Table 1).

Small Mammal Sampling

Near the center of each plot, we located a circular trap line (Calhoun, 1959) consisting of 40 trapping stations at 7.6 m intervals (25 ft). Two small mammal live

TABLE 1. Estimated abundance by median cover classes for each of the major plant groups on the three areas combined.[1]

Year	Treatment	Plant Groups		
		Grass	Forb	Shrub
1970	Untreated	4	2	2
	Treated	1	2	3
1971	Untreated	4	3	2
	Treated	1	2	3

[1]Cover classes were based on the percentage of each 1-mil-acre sampling plot occupied by one of these groups of vegetation. Cover classes by percentage plant cover were: 1, 0-5 percent; 2, 5-25 percent; 3, 25-50 percent; 4, 50-75 percent; 5, 75-100 percent.

traps (8 x 9 x 25 cm) were placed near each station, and one large (23 x 23 x 80 cm) welded-wire trap was placed at every other station. Populations of small mammals were sampled by mark-recapture and removal trapping procedures.

Mark-recapture trapping was designed to compare the composition and size of small mammal communities on each side of the test areas before application of herbicides and to study whether changes occurred after treatment. For three consecutive nights, animals were trapped, identified, ear-tagged, and then released. This procedure was repeated after herbicide application and at monthly intervals thereafter until removal trapping began in June of both years.

Removal trapping data were used for censusing the small mammal communities; for calculating removal rates, sex ratios, and age structures; and for estimating the species composition of the communities.

We conducted removal trapping for 30 days after the final three days of mark-recapture trapping each year. Because catches usually decline after one week of continuous trapping, traps were checked every other day after the first seven days.

Mark-recapture data from the first trapping periods in each year supported the assumption of homogeneity in species composition and number of small mammals on each area before herbicide applications.

Data were analyzed by pairing the numbers of individuals of each species caught on treated and untreated plots from each study area and each trapping period. The hypothesis that the mean of the differences between pairs equals zero was tested with Student's t-distribution at the 95 percent probability level (Snedecor and Cochran, 1967).

To analyze removal-trapping data, we constructed a "Davis graph" (Overton and Davis, 1969) to evaluate the various species' responses. Community responses were analyzed by a program that allows examination of changes in abundance, diversity, and relative species composition of the communities (Overton 1971).

Results and Discussion

Post-Treatment Vegetation

Herbicide treatments reduced competition from other vegetation and provided a more favorable environment for survival and growth of Douglas-fir seedlings. The treatments restructured abundance and diversity of the plant communities; those that had been dominated by perennial grasses and forbs consisted primarily of shrubs, forbs, and Douglas-fir after treatment.

Observations during and after herbicide application confirmed that herbicide coverage was complete. Grasses, the predominant plants, were affected most by treatment (Table 1); their abundance declined markedly in both years. After the second year of treatment, mean forb cover was reduced—primarily in frequency and cover class—although forbs varied widely in their response. Species such as western wood strawberry *(Fragaria bracteata)*, fragrant bedstraw *(Galium triflorum)*, false dandelion *(Hypochaeris radicata)*, Oregon iris *(Iris tenax)*, and sword fern *(Polystichum munitum)* appeared unaffected. Canadian thistle *(Cirsium arvense)*, slender thermopsis *(Thermopsis gracilis)*, and bracken fern *(Pteridium aquilinum)* increased in frequency and cover on treated plots.

Although some shrub species were damaged and suppressed initially, the reduced

competition for moisture through control of grasses promoted their recovery and subsequent vigor. The result was a small increase in shrub cover on treated plots.

All three untreated plots had a greater species diversity, primarily of forbs. Similar species of grasses and shrubs occurred on both sides of a test area.

Small Mammals

During annual censuses in 1970 and 1971, we caught a total of 1170 small mammals of 11 species. The principal species caught during removal trapping are shown in Table 2 by their relative proportions in the small mammal communities. Several other

TABLE 2. Five principal species of small mammals removed from the three study areas in both years and their percent of composition of the small mammal communities.

Area	1970				1971			
	Untreated		Treated		Untreated		Treated	
Species	Number	%	Number	%	Number	%	Number	%
Carlson Creek								
Sorex vagrans	30	39.5	11	17.5	5	11.1	1	2.2
Sorex trowbridgii	4	5.3	15	23.8	3	6.7	7	15.2
Peromyscus maniculatus	18	23.7	33	52.4	20	44.4	35	76.1
Microtus oregoni	19	25.0	—	—	9	20.0	1	2.2
Zapus trinotatus	2	2.6	—	—	4	8.9	1	2.2
TOTAL	73	96.1	59	93.6	41	91.1	45	97.8
Williams Creek								
Sorex vagrans	39	21.1	38	33.0	5	16.1	3	8.1
Sorex trowbridgii	7	3.8	11	9.6	3	9.7	2	5.4
Peromyscus maniculatus	30	16.2	26	22.6	12	38.7	27	73.0
Microtus oregoni	94	50.8	35	30.4	5	16.1	—	—
Zapus trinotatus	4	2.2	—	—	2	6.5	—	—
TOTAL	174	94.2	110	95.6	27	87.1	32	86.5
Maxfield Creek								
Sorex vagrans	40	14.3	14	12.4	28	23.7	7	11.5
Sorex trowbridgii	2	0.7	18	15.9	—	—	2	3.3
Peromyscus maniculatus	25	8.9	33	29.2	2	1.7	13	21.3
Microtus oregoni	174	62.1	37	32.7	52	44.1	22	36.1
Zapus trinotatus	34	12.1	3	2.7	34	28.8	14	23.0
TOTAL	275	98.2	105	92.9	116	98.3	58	95.1

species were infrequently caught in the large traps and released without marking at the trapping stations. However, California ground squirrels *(Spermophilus beecheyi)*, caught mainly during mark-recapture trapping, were removed from the areas.

Five species comprised more than 95 percent of the animals caught during removal trapping; Oregon vole *(Microtus oregoni)*, deer mouse *(Peromyscus maniculatus)*, vagrant shrew *(Sorex vagrans)*, Trowbridge shrew *(S. trowbridgii)*, and Pacific jumping mouse *(Zapus trinotatus)*. Because these species were abundant, we obtained useful data on their responses to changes in vegetation.

Rate of Removal. The time required to remove 50 percent of each species was the measure of removal rates. The mean numbers of days to remove each of the five most abundant species, with 95 percent confidence limits, were:

Peromyscus maniculatus	2.3 ± 1.2
Microtus oregoni	6.5 ± 2.1
Zapus trinotatus	7.0 ± 1.9
Sorex vagrans	12.5 ± 2.5
Sorex trowbridgii	13.4 ± 3.5

The time required to remove 50 percent of a species did not differ significantly between untreated and treated plots. The mean values, therefore, are based on all samples.

Calhoun (1964) proposed that small mammal communities have a well-organized social structure with dominant and subordinate species. He suggested that dominant species have a higher probability of capture because of some behavioral characteristic such as a large home range. Gentry *et al.* (1968) and Schamberger (1965) obtained results supporting Calhoun's theory of dominance.

Although abundance affects the expression of dominance and probability of capture, some subordinate species commonly outnumber dominant ones. This fact suggests that mark-recapture data limit estimates of abundance and relative species composition to dominant species and individuals, or at least to those with the highest probability of capture. Removal trapping of dominant species increases exposure to traps for subordinate species.

Our data also support Calhoun's theory. Obviously, some species were removed more quickly than others; for example, the deer mouse accounted for most of the catch during the first few days of removal trapping.

Shrews were scarce during the first few days of removal trapping but became more prevalent as the dominant species were removed. The Oregon vole appeared to have a constant rate of removal, generally relative to the abundance of the species in the community. This finding suggests that the vole is not influenced by the dominance hierarchy. Few Pacific jumping mice were taken during the first week of trapping, but their rate of removal was rapid thereafter.

Age Structure. Adults and subadults comprised the bulk of the small mammals handled. A few juveniles were captured, but because of their small numbers, subadults and juveniles were combined into one age group as subadults. Age structure did not differ significantly between untreated and treated plots. Percentages of adults and subadults, therefore, were calculated from the total capture for each species.

Adults accounted for 60 percent of the Oregon voles captured during removal trapping. Even greater percentages of deer mice and Pacific jumping mice were adults (86 and 98 percent, respectively).

On the other hand, 60 percent of the Trowbridge shrews and 58 percent of the vagrant shrews were subadults, although adult animals were predominant during mark-recapture trapping. A seasonal variation in the age classes of shrews taken by live trapping also was reported by Jameson (1955) and Findley (1955).

Sex Ratios. We assumed a 1:1 sex ratio for each of the five principal species. Evidence caused us to reject this hypothesis only for the deer mouse on treated plots. Significantly more male than female deer mice (2:1) were trapped on treated plots ($X^2 = 17.02$, $df = 1$, $P < 0.005$), possibly because males moved farther and thereby increased their probability of capture. Unequal sex ratios in studies of small mammals often are attributed to trap bias (Blair, 1940; Stickel, 1946). But Terman and Sassaman (1967) showed an aberrant sex ratio for *P. maniculatus* and speculated that aberrance, rather than trap bias, may explain the unequal sex ratios frequently observed for wild populations.

Deviation from the 1:1 ratio occurred within individual populations of other species, and it was more apparent at higher densities but not consistent.

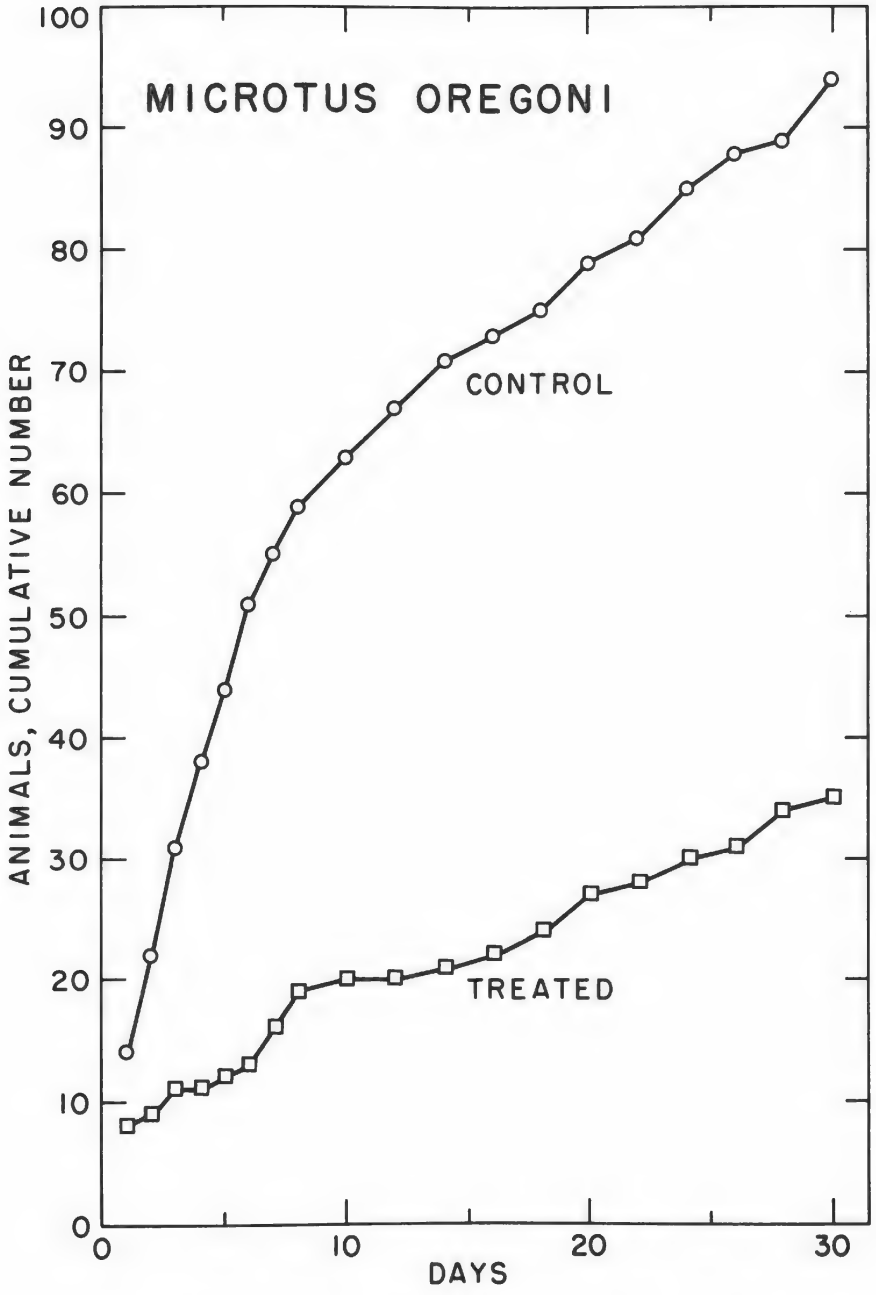

Figure 1. The cumulative number of *Microtus oregoni* removed from untreated and treated plots on the Williams Creek area in 1970.

Post-Treatment Populations. Small mammal communities on treated and untreated areas differed significantly only during the last period of mark-recapture trapping in each year, when vegetative conditions were most altered and analysis of variance showed that habitat manipulation with herbicides had a significant effect. As expected, significant differences were observed among areas and between years, and the degree and direction of community responses depended on species composition.

The Oregon vole was most abundant, comprising 38.3 percent of the 1170 animals removed. Herbicide-induced change in habitat reduced its population and decreased relative abundance in the communities. The response on all areas was similar to that for the Williams Creek area (Fig. 1). Seventy-nine percent of the 448 voles removed were captured on the three untreated plots.

Deer mice, the next most abundant small mammal, accounted for 23.4 percent of the captures. They responded to habitat change by increasing in abundance (Fig. 2).

The two species of shrews demonstrated opposite responses to herbicide-induced habitat change (Fig. 3). The Trowbridge shrew was the least abundant of the two, accounting for only 6.3 percent of the small mammals trapped; 74 percent of these shrews were taken on treated plots. The more abundant vagrant shrew accounted for 18.9 percent of the animals removed; 67 percent of these 221 vagrant shrews were taken on untreated plots.

The Pacific jumping mouse accounted for 8.4 percent of the mammals removed, but comprised a significant proportion of the community only at the Maxfield Creek area, where 87 percent of the 98 jumping mice were trapped. The Pacific jumping

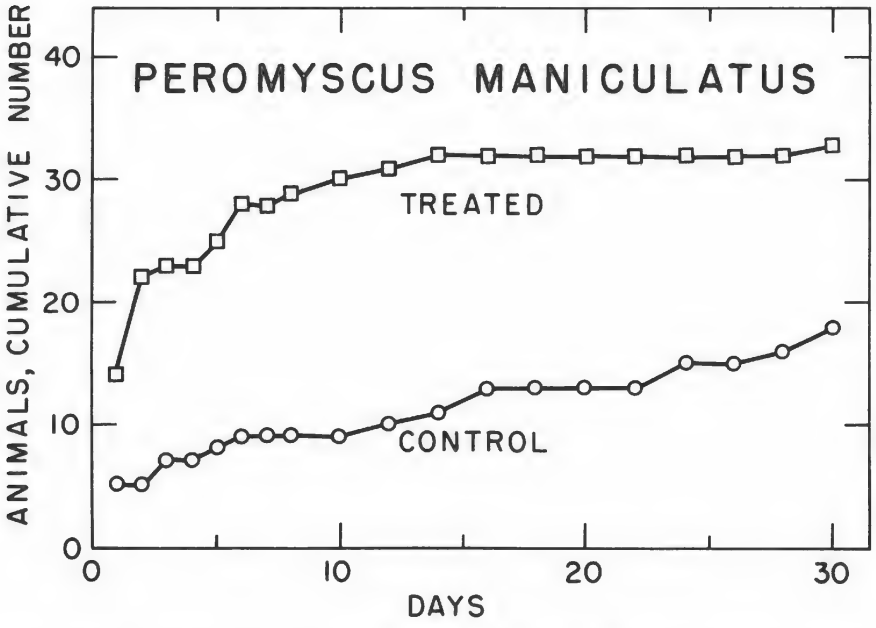

Figure 2. The cumulative number of *Peromyscus maniculatus* removed from untreated and treated plots on the Carlson Creek area in 1970.

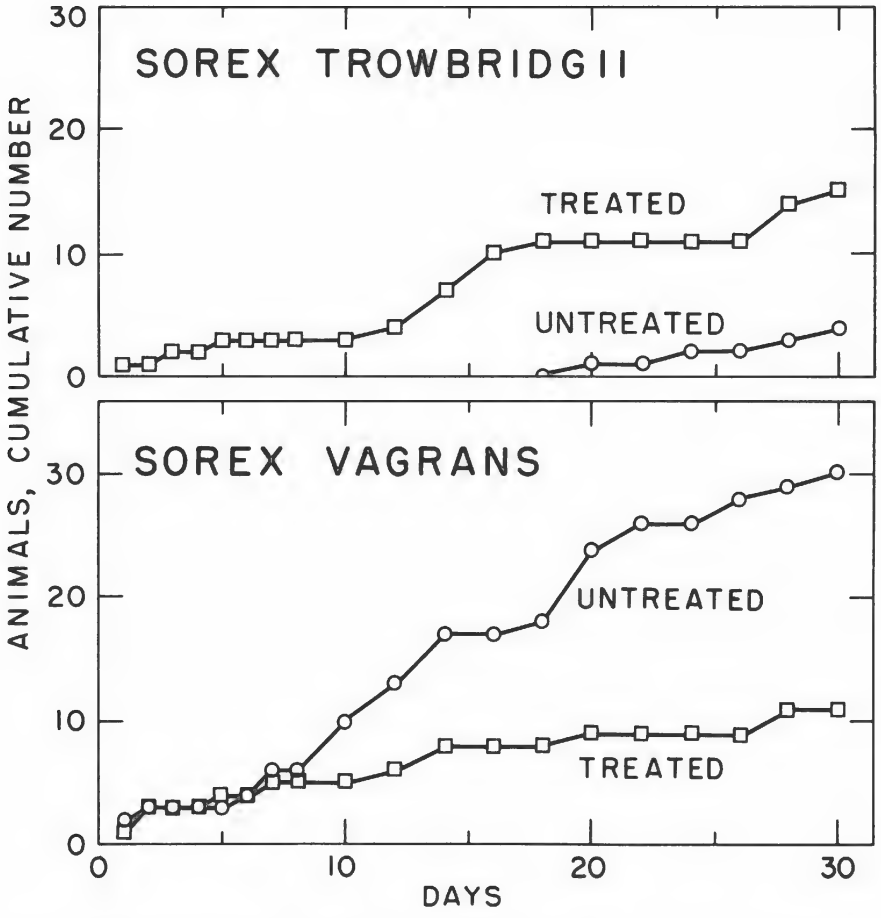

Figure 3. The cumulative numbers of *Sorex trowbridgii* and *S. vagrans* removed from untreated and treated plots on the Carlson Creek area in 1970.

mouse showed reduced abundance after treatment in much the same pattern as the Oregon vole and the vagrant shrew (Fig. 4).

Some species occurred together with greater frequency than others, which suggests similar habitat preferences but lack of direct competition or overlapping niches. Two groups were evident: one composed of the Oregon vole, vagrant shrew, and Pacific jumping mouse; the other included deer mouse and Trowbridge shrew.

The Oregon vole occurs in a wide range of habitats throughout the Pacific Northwest. It prefers ground cover of mixed grasses and forbs often associated with the seral vegetation of logged or burned areas (Goertz, 1964; Maser and Storm, 1970). The vagrant shrew prefers wet meadows. Findley (1955) reported that the ecological requirements of this species are similar to those of the Pacific jumping mouse, which occurs primarily in wet meadows, especially near a forest edge (Ingles, 1965). The

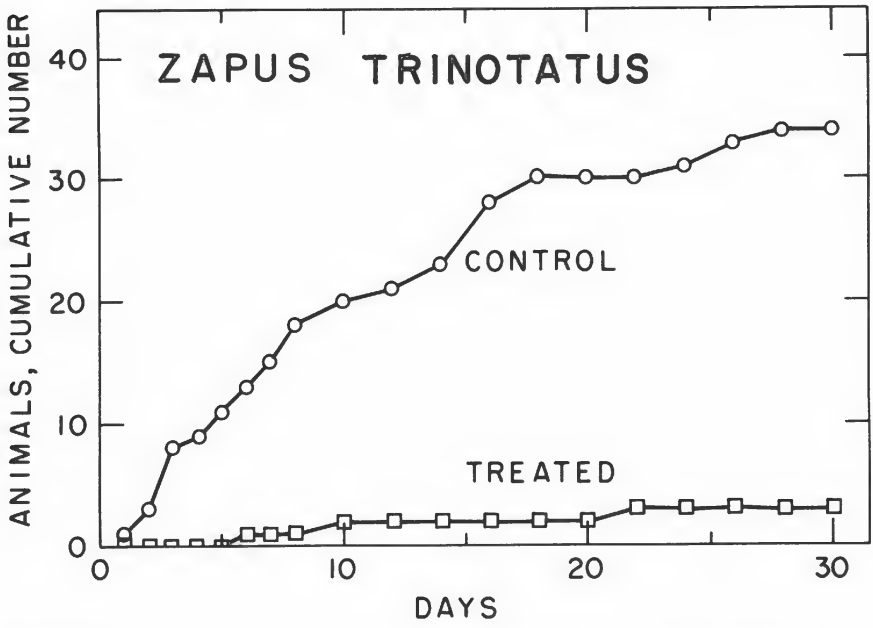

Figure 4. The cumulative number of *Zapus trinotatus* removed from untreated and treated plots on the Maxfield Creek area in 1970.

deer mouse is ubiquitous in North America, but chiefly inhabits brushy and forested sites (Baker, 1968; Hooper, 1968; Ingles, 1965). Few studies have been made of the biology and ecology of the Trowbridge shrew, but most researchers report its habitat is in litter on the floor of coniferous forests (Ingles, 1965; Jameson, 1955).

Considering the reported preferences in habitat for each species, we were not surprised that the restructuring of vegetation of test sites increased the carrying capacity of the habitats for deer mice and Trowbridge shrews and decreased the carrying capacity for the Oregon vole, vagrant shrew, and Pacific jumping mouse.

The number of species in a sample was fairly uniform among areas and between years and treatments. Differences were generally attributable to single or unlikely captures. The change in composition of small mammal communities was the most significant result of herbicide-induced habitat changes.

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Effects of Repeated Prescribed Burns on Northern Idaho Elk Browse[1]

Abstract

A seral shrub community was treated with three prescribed spring burns at five-year intervals. All shrub species responded with basal sprouts and/or seedlings following each burn. Results indicated that repeated spring burns at the recommended interval of 10 to 15 years would have little effect on density and composition of most species. However, redstem (*Ceanothus sanguineus*) will increase when seedlings survive, whereas bitter cherry (*Prunus emarginata*) may decrease because of adult mortality.

Introduction

Excellent winter ranges for elk (*Cervus elaphus nelsoni*) were created in northern Idaho when shrubs replaced conifers following wildfires in the early 1900s. However, with plant succession over time, these ranges have become less desirable for elk, and prescribed burning has been used to improve them since the mid-1960s (Leege, 1968). Primary reasons for burning are to (1) retard conifer dominance, (2) reduce the height of existing browse plants, (3) increase browse quality and palatability, and (4) stimulate forage plants to regenerate from seed. Studies have indicated that brushfields need to be repeatedly burned at 10-to 15-year intervals in order to maintain forage production at high levels (Leege, 1972). Questions have been raised about long-term effects of repeated fires on seral shrubs. As it would require many years to document changes from multiple 10-to 15-year treatments, I shortened the burning interval and measured some of the effects of three prescribed spring burns repeated at five-year spacings. I assumed that effects would likely be magnified by burning at shorter intervals than would normally occur in shrubfield management.

Study Area

A study area was chosen on a southwest aspect at 700 m elevation along the lower slopes of Fish Creek drainage, a major tributary of the Lochsa River in north-central Idaho. Slopes range from 35 to 50 percent and the soil developed from granitic parent material of the Idaho Batholith. Existing vegetation indicated that the area is in the *Abies grandis-Pachistima myrsinites* habitat type as described by Daubenmire and Daubenmire (1968). Common herbaceous species present included: false lupine (*Thermopsis montana*), bracken fern (*Pteridium aquilinum*), goatweed (*Hypericum perforatum*), yarrow (*Achillea millefolium*), and strawberry (*Fragaria vesca*).

The area was burned by wildfire in the summer of 1934 and again in the spring of 1954 (Pers. comm., L. Hartig, retired Forest Service employee). It was selected as the site of our experimental burns because it was accessible, harbored a variety of shrub species with few conifers, and had a good ground cover of bracken fern to assure a

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successful surface fire. However, the shrubs were atypically small compared to those commonly found on other seral shrub ranges in northern Idaho—presumably because most ranges have not been burned since 1934 or earlier. The area was used heavily by elk almost every winter during the study.

Methods

A seven-plot transect was established in the spring of 1965 prior to burning. Plots were spaced at 15-m intervals and marked with a metal reinforcing rod. Forty-five shrubs of ten different species were tagged and referenced by azimuth and distance to these plot stakes.

Each shrub was measured for maximum crown height, live crown diameter (average of two perpendicular measurements), percent dead crown, number of basal sprouts and average sprout height (first growing season after burning only).

Another stake was located 1.5 m to the left of each main plot stake and at an angle perpendicular to the transect line. Shrub seedlings were counted within a circle (.81 m^2) circumscribed around all 14 stakes. All measurements were taken immediately prior to burning and annually thereafter during late summer after annual twig growth was complete.

The study area was initially prescribed burned on 31 March 1965. Weather records at the Kooskia Ranger Station (54 km southwest at 384 m elevation) were as follows: maximum temperature—25°C, relative humidity at 1600 hrs—35 percent; westerly wind at 8 km/hr. Burning conditions were fair and shrubs were in dormant condition.

We reburned the area on 3 May 1970. Weather records at Kooskia were: maximum temperature—27°C; relative humidity at 1600 hrs—16 percent; wind negligible. Burning conditions were excellent. Plant phenology was more advanced than when the area was burned in 1965—small leaves were apparent on some shrub species.

The third prescribed burn occurred on 14 May 1975. Weather readings at Kooskia were: maximum temperature—31°C; relative humidity—27 percent; wind negligible. Leaves on shrubs and succulent herbaceous growth appeared to retard the fire, despite the excellent burning weather.

All three burns were ignited along the contour below the study area and a head fire was allowed to run through the plots. Burn coverage was complete on each occasion. Most of the dried herbaceous material was consumed and some mineral soil was exposed, especially by the last two burns.

Measurements were analyzed using an analysis of variance and Duncan's multiple range test to detect specific differences among treatments (Steel and Torrie, 1960). The word "significant," when used in reference to specific findings, indicates statistical probability at the .05 level.

Results and Discussion

Shrub Seedlings

Numerous redstem seedlings were observed on the study area in June of 1966, fourteen months after burning. However, when the plots were examined in August, 1966, no seedlings were found. The loss may have been caused by dry weather which occurred

between 1 May and 1 September. Only 78 percent of normal precipitation fell during that period (Table 1).

TABLE 1. Average monthly temperatures (C) and precipitation (cm) at the Fenn Ranger Station for the growing season months.

Year	May		June		July		August		Avg.	Total
	Temp.	Ppt.	Temp.	Ppt.	Temp.	Ppt.	Temp.	Ppt.	Temp.	Ppt.
1965	11.2	8.1	16.1	3.4	21.5	2.4	20.6	10.3	17.3	24.2
1966	13.9	2.9	15.6	9.9	21.5	0.1	21.3	3.9	18.1	16.8
1967	11.8	7.0	16.8	7.3	21.8	0.2	23.2	0.0	18.1	14.5
1968	12.6	8.1	16.3	7.3	21.3	1.1	18.8	8.1	17.3	24.5
1969	14.6	7.0	17.8	8.7	19.8	0.6	19.8	0.0	18.0	16.4
1970	13.0	5.9	19.2	8.1	21.6	2.5	20.8	0.0	18.6	16.5
1971	13.9	9.0	15.2	10.5	19.9	0.9	21.8	0.8	17.7	21.2
1972	*	6.5	17.7	6.6	20.6	3.5	21.9	2.5	*	19.1
1973	13.7	5.1	15.8	8.2	21.0	0.2	21.1	0.5	17.9	13.9
1974	12.1	7.4	18.8	7.7	20.5	3.2	19.8	2.6	17.8	20.9
1975	11.7	10.1	15.6	8.9	23.0	4.0	18.6	19.8	17.2	32.6
1976	14.3	7.1	15.3	11.3	20.9	5.7	18.8	5.8	17.3	29.9
Long-term Ave.	13.5	8.6	17.1	8.0	21.5	1.9	20.8	3.5	18.2	21.6

*Data missing

[1]Fenn R.S. is located 30 km SSW of the study area at 483 m elevation.

No shrub seedlings were again observed on the plots until June, 1971, 13 months after the second prescribed burn. Twenty-three redstem and three bitter cherry seedings were counted at that time. The plots were counted again in September of that year and only eight redstem and one bitter cherry remained. A year later in September, 1972, just four redstem were alive and, by the following September, all had died. Below-average rainfall during the May-August periods, 1971-73, may have influenced seedling survival (Table 1).

New shrub seedlings occurred on the plots in June, 1976, 13 months following the third prescribed burn: twenty redstem, two bitter cherry, and one serviceberry (*Amelanchier alnifolia*). The summer of 1976 was much wetter than usual; all seedlings, except for eight redstem, remained alive in September when the study terminated. Competition for moisture during the two years following germination appeared to be a significant factor affecting shrub seedling survival. Orme and Leege (1976) found that redstem survival was related to summer precipitation, aspect, elevation, and type of burn (fall vs. spring).

Shrub Mortality

Aerial portions of all marked shrubs were killed by each prescribed burn. All shrub species, except bitter cherry, sprouted following each fire. The seven bitter cherry plants sprouted after the 1965 burn with an average of 10.4 sprouts per plant. Only four of the seven sprouted after the second burn and two after the third burn in 1975. Another mortality occurred in 1976, for a total of 86 percent loss of the original seven shrubs. Fourteen percent of 36 bitter cherry plants died after single prescribed burns on two nearby areas (Leege and Hickey, 1971), so apparently mature plants are severely affected by fire, especially multiple burns. However, mortality may have been accentuated during this study because of the advanced plant phenology evident during the second and third burns. Hickey (1971) clipped redstem plants to ground level at various phenological stages and found that mortality was highest among plants clipped when flowering on 17 May. In South Carolina, Lewis and Harshbarger (1976) reported that

annual summer burning eliminated shrubs; however, dense stands of sprouting shrubs persisted on the periodic summer burns and on both the annual and periodic winter burns.

Sprouting

Sprouting was initiated within four to eight weeks following each of the three burns. For all species combined, the average number of sprouts decreased from 45.7 to 36.9 after the 1970 and 1975 burns, respectively (Table 2). This figure was not comparable with the 1965 burn because sprouts in excess of 50 were not counted in that year. The change in sprout numbers between 1970 and 1975 was not significant for all species combined, or for any single species. However, nine species showed decreases in sprout number while only one species, willow (*Salix scouleriana*), showed an increase.

Average sprout height decreased each time the area was burned when measurements for all species were combined (Table 2). However, the decrease was not significant because of the variation among species. Although seven of ten species had shorter sprout heights after the third burn, as compared with the second (1975 vs. 1970), none of the differences were statistically significant. Serviceberry and oceanspray (*Holodiscus discolor*) had significantly shorter sprouts when comparing 1965 with 1975.

The two years most comparable were 1970 and 1975 because in both cases the shrubs had only five years before burning to accumulate carbohydrate reserves. However, the 1975 burn was conducted when shrubs were more actively growing, and thus were more likely to be adversely affected by the burning treatment. On a nearby study area, Hickey (1971) found that redstem plants only produced about one-third the annual growth when clipped at the full-bloom stage (17 May) as compared with the bud-active stage (21 April). Phenology of most shrubs was closer to the full-bloom stage during the 1975 burn than in 1970. However, in 1975 and 1976 the summer precipitation was much higher than usual and probably had a compensating effect on shrub growth (Table 1).

Crown Size

For comparing crown dimension changes after burning, I selected the end of the second growing season following treatment—1966, 1971, and 1976. The average of all species indicated a downward trend in crown height following the three burns. However, the only significant change was with serviceberry between the 1966 and 1976 measurements, and 1971 and 1976 measurements (Table 2). Scouler willow and birch (*Betula papyrifera*) were the only species that did not show a decline in height after the third burn, as compared with the first. Two other species, mountain maple (*Acer glabrum*) and syringa (*Philadelphus lewisii*), did not show a decline between the second and third burns. Growth rate following the burns was very similar when average maximum crown heights of all species were compared for each year (Fig. 1).

Crown diameters did not show any consistent change after repeated burns. The only significant change was for birch where the diameter following the third burn was significantly greater than the diameter after the first burn (Table 2).

Conclusions

All shrub species produced sprouts following each treatment except bitter cherry, which suffered heavy mortality. However, this species replaced itself by generating seedlings

TABLE 2. Changes in shrub measurements after prescribed burns in 1965, 1970, and 1975[1].

Species	No. plants	Avg. 1965 preburn crown ht.	Avg. 1965 preburn crown dia.	Avg. no basal sprouts per plant '65	'70	'75	Avg. sprout height '65	'70	'75	Max. crown ht. 2 yrs. after burn '66	'71	'76	Max. crown dia. 2 yrs. after burn '66	'71	'76
Ceanothus sanguineus	10	177	79	35.4+	36.2	22.0	70	70	73	158	155	152	116	128	127
Salix scouleriana	10	241	158	46.7+	62.1	65.6	128	125	119	232	226	232	162	177	180
Amelanchier alnifolia	5	378	125	50.0+	149.4	112.2	94AB	67A	55B	183A	162B	134AB	140	134	128
Holodiscus discolor	5	262	85	33.4+	38.6	34.0	79A	70	55A	137	125	119	101	116	98
Betula papyrifera	3	524	98	31.3	58.3	55.0	94	98	91	253	259	259	116A	146	168A
Acer glabrum	2	283	85	50.0+	50.0	48.5	76	40	40	168	85	91	91	61	61
Rhamnus purshiana	1	244	91	18.0	12.0	7.0	91	76	76	183	137	122	137	107	107
Physocarpus malvaceus	1	137	46	21.0	21.0	4.0	61	61	46	91	76	61	46	46	46
Philadelphus lewisii	1	213	46	14.0	19.0	16.0	61	46	30	122	76	76	61	61	46
Prunus emarginata	7*	253	49	10.4	10.0	9.5	76	91	46	155	165	122	67	76	61
Avg.		271	86	—	45.7	37.4	83	74	63	168	146	137	104	105	102

[1]Letters A and B following measurements indicate a statistical difference at the .05 level from other measurements within the same group that have the same letter. All measurements other than sprout numbers are in centimeters.

+In 1965, basal sprout numbers in excess of 50 were tabulated as 50+. Therefore + indicates that one or more shrubs in the average had more than 50 sprouts but was only counted as 50.

*Seven bitter cherries were measured in 1965 and 1966, four in 1970 and 1971, two in 1975, and one in 1976.

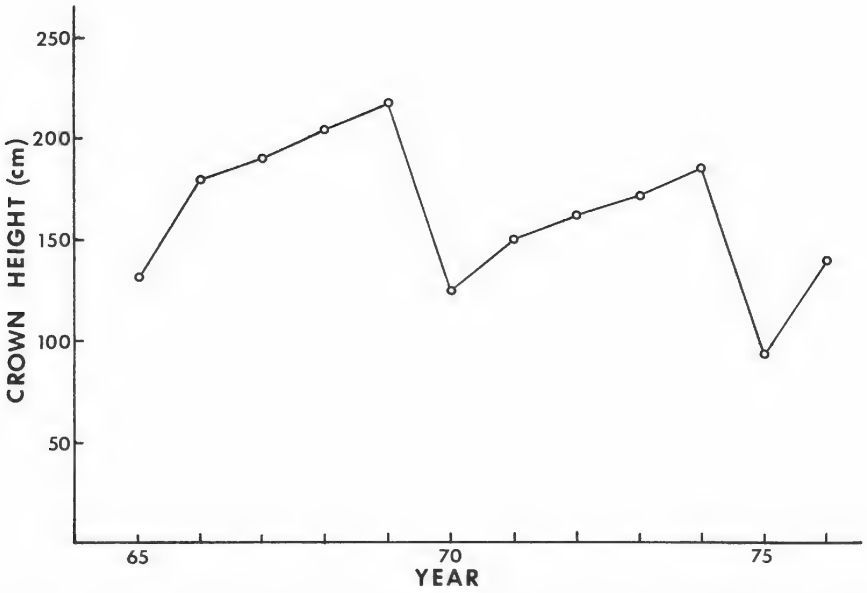

Figure 1. Average maximum live crown height of ten shrub species between 1965 and 1976. Measurements in 1965, 1970, and 1975 reflect crown height after one growing season following spring burning.

after each burn. Survival of seedlings was poor, but some new plants were likely being added to the plant community. Bitter cherry is not a preferred browse plant for deer or elk, so a decrease in plant density may actually increase the food supply by providing more growing space for desirable species.

If spring burning was continued at five-year intervals, results indicate that scouler willow, a very desirable browse plant, and birch would maintain their position in the plant community. Redstem, the major constituent of the elk winter diet in this area (Trout and Leege, 1971), may increase in density because of the occurrence of new seedlings after each burn. Since mature redstem plants bear fruit within two years after they are spring-burned (Leege, unpublished data), a continual supply of redstem seed is assured.

There were indications that other species were reduced in vigor following repeated burning; however, few of the recorded differences were significant because of small sample sizes and variable responses among individuals of the same species. Sprout numbers and sprout height were, for most species, less in 1975 than 1970, despite the growing season of 1975 having twice the precipitation of 1970. Reduced growth in 1975 was probably related to stage of phenology at which the shrubs were burned in May of 1975, and/or lower carbohydrate reserves than prior to the 1970 burn. A gradual reduction in density of these species may occur if burns are repeated at short intervals for an extended period of time, especially if shrubs are burned when actively growing.

Findings from this study cause me to speculate that if spring burns were conducted at the more normal interval of 10 to 15 years, instead of every five years, changes in

shrub composition and density would occur very slowly, if at all. Whereas, if no burning occurred, density of all shrub species would decrease as forest succession advanced and conifers assumed dominance. Redstem would be among the first species to disappear since it is very intolerant of shade (Leege and Hickey, 1975).

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Observations on Reproduction of Mountain Caribou

Abstract

Aspects of reproduction of the West Kootenay band of mountain caribou are described. Four or five calves are produced yearly by this band of about 25 animals. Behavior of the rutting band, sequence of antler development and loss, and apparent occurrence of suckling by a yearling are described. The only confirmed calf mortalities have resulted from collisions with motor vehicles. Recruitment compares favorably with that of other stable caribou populations, but it would not compensate for even a slight increase in mortality for this small population.

Several aspects of the reproductive biology of mountain caribou *(Rangifer tarandus montanus)* in the Kootenay Pass region of British Columbia have been observed since 1972. About 25 caribou occur in the vicinity of the pass; a few others occur farther south in northern Idaho and northeastern Washington. Our observations on reproduction were made incidental to studies of other aspects of caribou ecology.

Most caribou in the Kootenay Pass region occur in a single band during late winter and early spring. This group consists of both sexes and all age groups. Bulls disperse from this aggregation in early May and remain segregated as single animals or groups of two or three until the rut. Following calving, which apparently occurs in late May and early June, cows, calves, yearlings, and a few attendant bulls remain primarily in the Summit and Carolina Creek basins throughout the summer months.

Encounters with this group have enabled us to estimate the number of calves produced yearly since 1972 (Table 1). Since repeated counts by independent observers were often identical, we believe that these are accurate estimates of calf production. There is no confirmed evidence of calving south of the International Boundary (Freddy, 1974); but single cows with calves have been sighted in northern Idaho in September and November (A. Dargan and E. Bierman, pers. comm.).

The first evidence of pre-rutting behavior occurs in early September when bulls engage in mild sparring. Large bulls at this time possess polished antlers. We usually found antler-rubbed trees, 2-3 m in height, in small clearings on benches or on moist ground in the head of cirques. Most of these (80 percent) were subalpine fir *(Abies lasiocarpa)*. The remainder were Engelmann spruce (*Picea engelmanni*) and white-barked pine *(Pinus albicaulus)*. Additional damage to small trees probably resulted

from brush thrashing (Lent, 1965a), but we did not observe this behavior. Most antler-rubbed trees die as a result of this damage.

TABLE 1. Calf production and survival. West Kootenay Band.

Year of Birth	Number	Source and Date
1972	4	Darkwoods Ltd. personnel, 10 May 1973
1973	5	G. Schroeder, 9 August 1973
	4	D. Freddy, 20 March 1974
1974	5	Woods and Thompson, 31 July 1974
	5	G. Leslie, 10 February 1975
1975	4	R. Silver, 24 July 1975
	2	J. Martin, 26 April 1976
1976	5	The sum of a road-kill 4 July 1976 and 4 seen by R. Kerr, 29 November 1976

We consider mid-October the peak of the rut. Freddy (1974) found evidence of active spermatogenesis in a large bull shot on Kootenay Pass in late October (found 31 October and dead several days). We observed a rutting band at the headwaters of Lost Creek on 17 October 1974, consisting of a large dominant bull, three mature cows, two yearling cows, and two subordinate bulls. This group moved to the head of a cirque in the early morning and remained there throughout the day. The large bull paid close attention to one of the cows, which he periodically attempted to mount. He kept the other bulls at a distance of 15-20 m using head threats and sometimes by rushing at them. The tended cow occasionally rubbed her head against him. The bull regularly emitted a grunting sound; Bergerud (1973) has described this sound as a hoarse, gutteral pant. The band moved to level ground in the late afternoon and the dominant bull mounted the cow for 5-7 seconds. She offered some resistance, and we could not be sure that copulation had taken place, although Bergerud (1974) has identified successful mounts which were this brief. The cow terminated contact by kicking with both hind feet. We were able to bring the bull into close range by imitating his grunting sounds.

Based on counts of large bulls with renewed antler growth in late spring, we believe that there are at least three rutting groups in the vicinity of Kootenay Pass. We have reports of such bands in the headwaters of Curtis Creek (1975) and Hidden Creek (1977). There is considerable movement between groups, especially by subordinate bulls. Most rutting activity subsides in late October when the large bulls begin losing their antlers. There is progressive antler loss throughout the winter and spring by medium-sized and finally smaller bulls. We recovered a freshly dropped antler of a small bull on 14 April.

Antler formation and loss by cows is less predictable and influenced by pregnancy (Lent, 1965b; Skoog, 1968). Mature cows which are not pregnant shed first, usually in April. We have seen single-antlered cows in mid- and late April along with several which were antlerless. Some of these may have been older, barren cows. Although a few non-gravid cows retain their antlers into the calving season, most of those which carry antlers at calving are pregnant. Counts of antlered cows at calving then provides an estimate of natality (Skoog, 1968). Such a count would be unreliable for the West Kootenay band, however, because of their small number. Dennis Money photographed 18 animals near Kootenay Pass on 30 April 1974, of which only three cows were

antlered (two of these with a single spike). At least five calves were produced that spring (Table 1), more than we could anticipate based on the count of antlered cows prior to calving.

We have little information on the ovarian cycle in this population. A single corpus luteum was found in the ovary of a mature cow killed in a collision with a motor vehicle on 12 November 1976. It measured 10 mm in diameter, a value within the range of corpora lutea of pregnancy (Dauphiné and McClure, 1974). We could find no embryo in the uterus, an indication of a very recent pregnancy or perhaps a "silent heat." Ovarian cycling has been studied by McEwan and Whitehead (1972), who report estrous cycles of 10-12 and 24 days in captive animals.

Although the calves of Alaskan caribou are weaned by mid-September (Skoog, 1964), a few yearlings are known to suckle, even after their mothers have given birth to other calves (Lent, 1966). We encountered a mature antlerless cow with an enlarged udder, accompanied by a yearling cow, on 20 August 1975. Although we did not see the yearling suckle, we cannot explain the enlarged udder for any other reason unless the cow had recently lost her calf. Nursing by female yearlings would be more likely than by males since the former maintain a longer association with their mothers (Lent, 1966; Kelsall, 1968).

Only two instances of calf mortality have been confirmed, both as a result of collisions with motor vehicles along B.C. Highway 3 near Kootenay Pass (Freddy, 1974; Johnson and Todd, 1977). Gary Schroeder saw a calf limping in August, 1973. The calf count by David Freddy the following spring was one less than that Schroeder observed (Table 1), possibly an indication of its eventual death.

Recruitment, as measured by the proportion of calves in the population, reflects both pregnancy rates and calf survival. Recruitment in North American caribou populations usually ranges from 10-25 percent (summary by Parker, 1972). In a population of 25 animals, four or five calves such as that produced by the West Kootenay band would seem adequate for stability, given the present mortality rates. This recruitment would not compensate for even a slight increase in mortality for this small population.

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Trace Elements in a Columbia River Food Web

Abstract

The concentrations of several trace elements were measured by neutron activation analysis in caddisfly larvae and whitefish from the Columbia River. These concentrations were compared with previously measured levels in water and phytoplankton to examine trophic level relationships.

Concentrations of the majority of trace elements (Ag, Co, Cr, Cs, Fe, Na, Sb, Sc, and Zn) decreased through the food web. Potassium was the only element which increased in concentration, and four elements (Br, Hg, Rb, and Se) remained relatively constant. It was not possible to make generalizations, either seasonally or within tissues, concerning trace element concentrations in whitefish flesh, liver, and kidney. Comparison of these data with other published information reveals the complexity of food web relationships and the difficulty in extrapolation of data.

Introduction

Many data have recently been published concerning trace element analyses of a variety of environmental samples (e.g., Lucas *et al.*, 1970; Merlini *et al.*, 1969; and others). Few, however, have appeared concerning levels of trace elements in aquatic food webs—in particular, attempts to interpret the passage of trace elements through trophic levels. Mathis and Cummings (1973) presented data on selected metals in components of the Illinois River ecosystem, and Cushing and Rancitelli (1972) reported trace element analyses of Columbia River water and phytoplankton. Elwood *et al.* (1976) published data on trace elements in crane fly larvae (*Tipula* spp.), their gut contents and food (detritus), and interpretation of what they term the "trophic-transfer factor" (TTF) of various elements. Nomminga and Wilhm (1977) reported concentrations of various trace metals in water, sediments, and chironomid larvae.

As an extension of earlier work (Cushing and Rancitelli, 1972), I now quantify concentrations of the same elements reported previously from Columbia River water and phytoplankton in two higher trophic levels, namely the filter-feeding caddisfly larvae (Hydropsychidae) that ingest filtered phytoplankton, and whitefish *(Prosopium williamsoni)* that feed on caddisfly larvae by picking them from rocks or taking them as drifting organisms dislodged by the current. Combination of these data sets provides insight into the passage of various elements in the water→phytoplankton→caddisfly larvae→whitefish food web. Data are also presented on the distribution of various elements in whitefish flesh, kidney, and liver.

Methods and Materials

As described more fully by Cushing and Rancitelli (1972), attempts were made in 1970 and 1971 to collect the caddisfly larvae and whitefish samples at "ecologically significant" times of the year. These represented times of relatively long, stable environmental conditions (winter, summer) or periods of relatively rapidly changing

conditions (spring and fall phytoplankton bloom periods, summer high water). Unfortunately, the schedule was adversely affected by unusual water conditions in 1971. Abnormally high water levels allowed sampling of caddisfly larvae only once, and whitefish were unobtainable in June and August.

All samples were collected from the Columbia River within the Hanford Reservation, but upstream from all effluents associated with the reactors. It is not known to what extent whitefish may have been subjected to plant effluents, but it is known that they may seasonally move several kilometers upstream (Cushing and Watson, 1966). The sampling station was located at River km 616, about 2 km above and across the river from the furthest upstream operating reactor.

Caddisfly larvae were collected by handpicking organisms from rocks. Larvae were frozen immediately with dry ice and kept frozen until neutron activated prior to analysis. Caddisfly larvae were analyzed with gut contents included since we were interested in the total element transfer to the whitefish, not just that included in the larval tissues or adsorbed to the organism (see Elwood *et al.* [1976] for further details on this aspect). Whitefish were collected in the same vicinity by angling and also were frozen until neutron activated. Analyses were performed on composite samples of whitefish flesh from six to eight fish, and on flesh, liver, and kidney of an individual fish from each of the four samplings.

Concentrations were determined by neutron activation analysis. The basic procedures for irradiation and subsequent separation and gamma spectroscopy were described by Rancitelli and Tanner (1969). Elements analyzed in both caddisfly larvae and whitefish were Ag, As, Au, Br, Co, Cr, Cs, Fe, Hg, K, Na, Rb, Sb, Sc, Se, and Zn. In addition, Eu, Hf, La, Sn, Ta, Tb, and Th were measured in caddisfly larvae.

Results and Discussion

Table 1 presents the elemental concentrations in caddisfly larvae and whitefish flesh on 16 November 1970, together with similar data from water and phytoplankton collected at about the same date two years earlier. Based on these results, K is the only element increasing in concentration through the food web from phytoplankton to whitefish flesh. Nine elements, occurring in all three trophic levels (Ag, Co, Cr, Cs, Fe, Na, Sb, Sc, and Zn), decreased in concentration, some more significantly than others; e.g., Ag as compared to Na. Levels of Br, Hg, Rb, and Se remained relatively constant. Seven elements were detected in caddisfly larvae only; two in water, caddisfly larvae, and whitefish only; and three in water only (Table 1).

The above comparison involves only concentrations of the elements in the flesh of whitefish; but varying levels of several elements were found in other tissues of the fish. Table 2 shows concentrations of 17 elements in the flesh, liver, and kidney of a single whitefish from each of the four sampling trips. In essence, there are two "fall" samples (16 November 1970 and 14 December 1971), one winter sample (18 February 1971), and one spring sample (15 April 1971). Sample collection by angling was unsuccessful in mid-summer.

Examination of these data shows that generalizations cannot be made either seasonally within a tissue or among the three tissues. For instance, Cs and Rb are remarkably constant both seasonally and among tissues, but Fe reflects a two order of magnitude difference among the tissues. Several elements have unusually high or low

concentrations in a particular tissue on one sampling date; e.g., Sc in kidney, Zn in flesh. How much variation is attributable to true seasonal differences or to individual variation is difficult to ascertain, since only the values for flesh can be compared with composited samples from several fish taken at the same time. The composited values are shown in parentheses in Table 2. Agreement between composited and individual samples is good. It is not surprising to find inconsistencies when comparing such values considering the many variables involved—for example, age, previous exposure to effluents, etc.

TABLE 1. Elemental concentrations in Columbia River water, phytoplankton, caddisfly larvae, and whitefish flesh.

Element	ppb Water (11/14/68)	Phytoplankton (11/14/68)	ppm dry weight Caddisfly larvae (11/16/70)	Whitefish flesh (11/16/70)
Ag	0.50	0.93	0.039	<0.0015
As	2.5		0.0034	<0.82
Au	0.03		<0.016	<0.0057
Br	5.6	17.7	12.0	9.85
Co	0.02	9.11	0.87	0.022
Cr	0.40	22.8	1.8	<0.11
Cs	0.35	2.11	0.22	0.08
Cu	2.6			
Eu			0.056	
Fe	13.0	19200	2000	17.0
Hf			0.41	
Hg	<0.1	0.56	<1.0	0.405
K	1190	10700	12600	21000
La			1.6	
Mn	2.8			
Na	2200	8000	3900	1650
Rb	3.5	69.0	18.0	17.0
Sb	0.24	0.79	0.11	0.004
Sc	0.002	5.98	0.50	0.0003
Se	0.2	1.77	1.2	1.25
Sn			<12.0	
Ta			0.068	
Tb			0.066	
U	0.7			
Zn	8.0	1310	260	13.0

Comparison of these data with other studies is at best tenuous because of the varying analytical techniques, environmental conditions, sample handling, food, species, and so forth. The following discussion attempts to place the present data into some perspective.

Table 3 presents data on elemental composition of caddisfly larvae and a fish, the red-sided shiner *(Richardsonius balteatus)*, from the studies of Davis *et al.* (1958) in the Columbia River and this study. Values for Cr, Fe, and perhaps Co are similar for caddisfly larvae; however, our value for Zn is at least two orders of magnitude higher. Similar values for Cr and higher concentrations of Fe and Zn occur in the whitefish.

Mathis and Cummings (1973) reported analytical values for various elements in the flesh of five carnivorous fish species and five omnivorous fish species from the Illinois River near Peoria, Illinois. Although no whitefish were collected, the mean values for each of the two groups are compared with our data in Table 4 for three elements measured in common (see Mathis and Cummings [1973] for individual

TABLE 2. Elemental analyses of flesh, liver, and kidney from individual whitefish; values for composited flesh samples shown in parentheses.

Element	Flesh				Liver				Kidney			
	11-16-70	2-18-71	4-15-71	12-14-71	11-16-70	2-18-71	4-15-71	12-14-71	11-16-70	2-18-71	4-15-71	12-14-71
Ag[a]	5.1	<1.0		<1.0	110.2	28.0	240.0	160.0	91.0	12.0		53.0
	(<1.5)	(<1.3)		(<1.0)								
Au[a]	<5.8	<4.7			<12.0	<4.3			<21.0	<14.0		
	(<5.7)	(<6.6)										
Co[a]	22	35	32	17	200	420	200	220	1700	1700	640	880
	(22)	(24)	(33)	(67)								
Cr[a]	<240	<97	380	740	520	<100	<200	860	5200	430	780	12000
	(<110)	(135)	(170)	(<190)								
Cs[a]	90	53	98	61	49	47	44	59	46	27	44	68
	(80)	(59)	(75)	(51)								
Sb[a]	4.4	0.65	6.4	2.9	6.1	12.0	8.5	28.0	32.0	18.0	480	57.0
	(3.6)	(<.80)	(8.2)	(2.2)								
Sc[a]	<0.05	<0.05	<0.05	0.2	0.31	0.23	0.39	1.6	5.8	2.8	4.0	19.0
	(0.26)	(<0.05)	(0.16)	(0.2)								
As[b]	<1.3	0.61	1.4	0.94	<2.0	1.9	<4.0		1.8	<2.6	4.0	
	(<0.82)	(<0.86)	1.6	(<1.0)								
Br[b]	8.2	9.0	31.0	19.0	38.0	44.0	53.0	57.0	52.0	49.0	53.0	65.0
	(9.9)	(9.0)	(23.0)	(22.0)								
Cd[b]					10				104		5.3	
Fe[b]	17	23	38	17	220	750	150	32.0	690	1400	760	1300
	(17)	(18)	(33)	(24)								
Hg[b]	0.53	0.29	0.82	0.72	3.8	0.85	0.58	6.7	29.0	4.1	2.6	76.0
	(0.41)	(0.28)	(0.71)	(0.45)								
K[b]	22700	17800	19000	19100	19200	12700	13700	15200	15900	9900	19200	21700
	(21000)	(18200)	(19800)	(17600)								
Na[b]	1400	1200	5800	3000	3600	3800	5400	7200	4800	3700	5900	6700
	(1650)	(1200)	(3300)	(3500)								
Rb[b]	16	11	24	20	24	16	17	20	15	12	19	21
	(17)	(14)	(24)	(13)								
Se[b]	1.3	1.0	1.2	1.2	8.2	11.0	3.5	7.1	28.0	20.0	8.5	39.0
	(1.3)	(1.2)	(2.1)	(1.3)								
Zn[b]	13	11	42	19	91	84	140	260	120	57	97	89
	(13)	(11)	(26)	(24)								

[a]ppb dry wt.

[b]ppm dry wt.

species data). Zinc values are similar, but concentrations of Cr and Co are an order of magnitude less in Columbia River whitefish. The Illinois River receives considerably more domestic and industrial wastes than does the Columbia as reflected in the water concentrations shown in Table 4. Although this fact may partially explain the higher Cr and Co values in the Illinois River, it does not explain the similar Zn values. Since none of the data reported by Mathis and Cummings (1973) were from whitefish, the varying physiological demands among the species undoubtedly influences the levels found.

Table 5 presents comparative data for liver concentrations of two species of lentic whitefish (data averaged) from Lakes Michigan and Superior (Lucas *et al.*, 1970) and this study. Comparison shows values to be similar for Co and Zn, but considerably higher for As, Br, and Cd in Columbia River whitefish. No information is given for levels of these elements in the food of the Great Lakes fishes.

Comparison of trophic level changes is complex and certainly not straightforward (Enk and Mathis, 1977). The majority of elements measured in phytoplankton, caddisfly larvae, and whitefish flesh from the Columbia River decreased in concentration in this food chain. Conversion of data given by Mathis and Cummings (1973) to dry weights reveals that Cu, Ni, Pb, Cr, and Zn concentrations increased from sediments

TABLE 3. Elemental concentrations in Columbia River fish and caddisfly larvae (ppm dry weight).

	Caddisfly larvae[a]		Fish	
Element	Davis et al. (1958)	This study	Davis et al.[b] (1958)	This study[c]
Cr	2.04	1.8	0.20	0.152
Co	<0.52	0.87	<0.52	0.037
Fe	1534	2000	2.04	23.0
Zn	<5.11	260	<5.11	18.5

[a]Hydropsychidae

[b]**Richardsonius balteatus** (whole fish minus gut contents)

[c]**Prosopium williamsoni** (flesh)

TABLE 4. Elemental concentrations in Columbia River and Illinois River water (ppm) and fish (ppm wet wt.).

	Columbia River		Illinois River		
				Fish	
Element	Water	Fish	Water	Carnivorous	Omnivorous
Cr	0.0004	0.03	0.021	0.12	0.22
Co	0.00002	0.01	0.003	0.10	0.10
Zn	0.008	4.20	0.031	3.49	5.02

TABLE 5. Elemental concentrations in whitefish livers (wet weight).

Element	Columbia River (**Prosopium williamsoni**)	Lake Michigan (**Coregonus clupeaformis**)	Lake Superior (**C. clupeaformis** + **P. cylindraceaum**)
Co	59 ppb		47 ppb
As	500 ppb	21 ppb	6 ppb
Br	11 ppm		0.3 ppm
Cd	2.3 ppm	0.09 ppm	0.4 ppm
Zn	33 ppm		28 ppm

to oligochaetes and that Li, Co, and Cd were essentially unchanged. All elements decreased in concentration in carnivorous fish flesh, although specific food items are not mentioned. Rabe and Bauer (1977) found that trace metals generally decreased in concentration from sediments to chironomid larvae to yellow perch flesh. Namminga and Wilhm (1977) found that concentrations of Cu and Zn increased and Cr and Pb decreased from sediments to chironomid larvae which also ingest sediments. Dean (1974), conversely, found that tubificid worms did not accumulate ^{65}Zn, ^{51}Cr, ^{54}Mn, ^{46}Sc, ^{137}Cs, or ^{59}Fe from sediments, but did accumulate ^{51}Cr, ^{60}Co, and ^{65}Zn from water containing dissolved radionuclides. Sediments have been shown to act as "sinks" for many contaminants including trace metals (Enk and Mathis, 1977; Mathis and Kevern, 1975; Mathis *et al.*, 1977; Cushing, unpublished) and radionuclides (Brungs, 1967; Robertson *et al.*, 1973).

Elwood *et al.* (1976) studied the relationship between the gut contents (detritus) and body burdens of trace elements in crane fly larvae. Their data allow comparison of elemental concentrations between (1) crane fly larvae with and without gut contents, and (2) larvae with gut contents and detritus, and (3) larvae without gut contents and detritus. Differences occur in increases or decreases in concentration of certain elements, but the second case is analogous to the phytoplankton-caddisfly larvae analyses in this study. Comparison of their data with that of this study shows that roughly twenty-two elements increased in concentration, seven decreased, and one was essentially unchanged in the crane fly larvae. In caddisfly larvae, one element increased, nine decreased and four were unchanged. Elwood *et al.* (1976) further calculate a trophic-transfer factor (TTF) which is a ratio indicating whether there is food chain enrichment from detritus to crane fly larvae without gut contents. A preponderance of elements had TTFs less than unity, indicating a decrease between trophic levels. Recalculation of these data, using crane fly larvae with gut contents, reveals that three times as many

TABLE 6. Biomagnification factors, $\frac{\text{concentration in organism}}{\text{concentration in food}}$ (dry weight).

Element	Tipula[a] / Detritus	Oligochaete / Sediment	Chironomid / Sediment	Caddisfly / Phytoplankton
Ag				.04
Br	3.3			.7
Co	1.3	.9[b]		.1
Cr	.4	2.0[b]	.4[d]	.1
Cs	1.7			.1
Fe	1.7			.1
K	1.8			1.2
Mn	1.3	.3[c]		—
Na	344			.5
Rb	—			.3
Sb	—			.1
Sc	1.5			.1
Se	2.1			.7
Zn	2.9	1.7[b]	3.6[d], .1[e]	.2

[a]Calculated from Elwood **et al.** (1976) using **Tipula** spp. with gut contents.

[b]Calculated from Mathis and Cummings (1973) after converting oligochaete data to dry weight using a factor of 3.3279.

[c]Same as (b) above from Mathis **et al.** (1977).

[d]From Namminga and Wilhm (1977).

[e]From Rabe and Bauer (1977).

elements show higher concentrations in the crane fly larvae than in the detritus. This point further emphasizes the contribution which gut contents make to total element transfer in food webs. Comparison of absolute values revealed that elemental concentrations in the crane fly larvae and caddisfly larvae were remarkably similar on a dry weight basis, and that concentrations in phytoplankton were considerably higher than in the detritus. This finding partially explains the larger number of elements decreasing in the phytoplankton-caddisfly larvae link.

Table 6 gives selected biomagnification factors for elements for which comparable data are available. The most obvious difference is in the predominance of values >1, indicating biomagnification, in the data from Elwood *et al.* (1976) as compared to nearly all values of <1 in the data from the Columbia River. Potassium is the only element for which data are available from more than one study that exhibits the same response, a value >1. Chromium decreased and Zn increased at three of the four sites.

These data emphasize the complexity of food web relationships and indicate that extrapolation of data among organisms and sites should be made with caution. In Table 6, for instance, we are comparing biomagnification factors for invertebrates from their respective food bases, but it includes at least four different organisms and three distinctly different foods. Comparisons such as these, however, may be useful in identifying general trends in the dynamics of nutrient cycling.

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Population Dynamics of Wintering Bald Eagles on the Nooksack River, Washington

Abstract

Seventy ground censuses were conducted during 1975-76 and 1976-77 to determine the population dynamics and distribution of wintering bald eagles (*Haliaeetus leucocephalus*) on the Nooksack River in northwest Washington. Eagles congregate between October and March on a 25-mile stretch on the upper reaches of the river. A population peak of approximately 100 birds occurs in January. During these two seasons, subadult percentages were 36 and 32, respectively. Salmon (*Oncorhynchus* spp.) was the primary food source and was most influential on eagle distribution patterns.

Introduction

An estimated 8000 to 9000 bald eagles winter in the contiguous United States (Spencer, 1976). Considerable research has recently described wintering populations in the interior states (Southern, 1963, 1964; Grewe, 1966; Edwards, 1969; Jonen, 1973; McClelland, 1973; Shea, 1973; Lish, 1975; and Steenhof, 1976); however, detailed studies on coastal populations are lacking. In the Pacific Northwest, large traditional populations congregate in the Gulf Islands of British Columbia, and on the San Juan Archipelago and the Skagit and Nooksack rivers of Washington.

Serious declines have occurred in most populations in the conterminous states (Sprunt, 1969). Documentation of all populations is needed to enact proper management procedures for this threatened species, especially in the Pacific Northwest. This paper reports on the population dynamics of a winter bald eagle population on the Nooksack River in Washington.

Study Area

The Nooksack River is located in northwestern Washington in Whatcom County (Fig. 1). The study area includes a 25-mile stretch of the north and middle forks and part of the mainstream. Most of the land in the study area is under private ownership.

Human influences in the study area are particularly prevalent. Logging, housing, mining, recreational developments, and recreational use, especially sport steelhead (*Salmo gairdneri*) fishing, are common activities.

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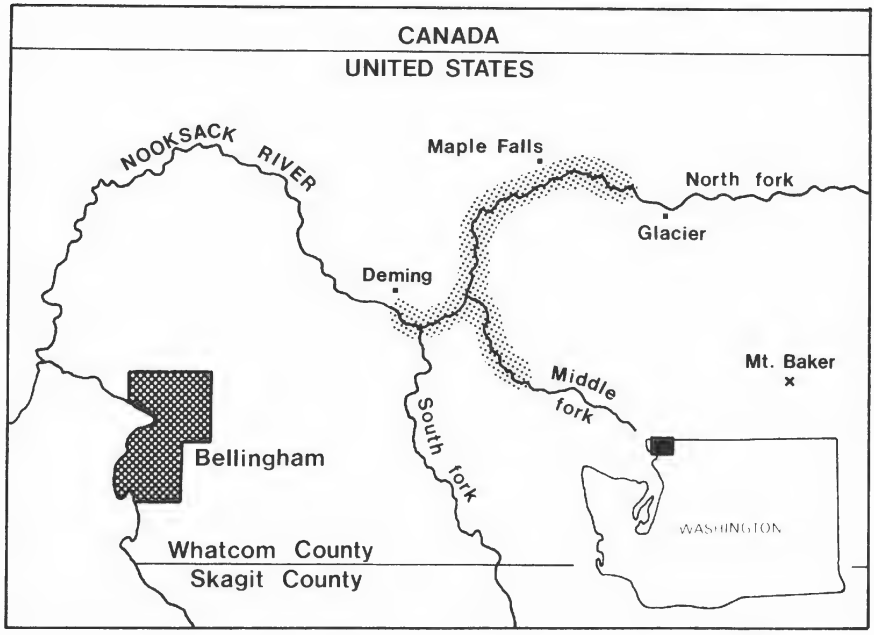

Figure 1. Location of the Nooksack River study area (stippled).

Dominant vegetation along the Nooksack River includes red alder (*Alnus rubra*) and black cottonwood (*Populus trichocarpa*). Surrounding forests are composed of Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*).

Methods

Preliminary population sightings were made during the wintering season of 1974-75 to locate the major concentration and to establish a census route. In 1975-76, 44 semi-weekly censuses were made; 26 weekly censuses were conducted in 1976-77. Several counts were also made in 1977-78. Censuses were conducted by driving and/or walking to predetermined observation points in the study area. Censuses began one to two hours after sunrise and lasted four to six hours.

Eagles were cataloged according to six age classes as described by Southern (1964, 1967) and Servheen (1975). Six-year-old birds (Southern's Plumage F) were classified as adults. Subadults of unknown age were grouped as subadults. Analysis of variance, employing a randomized block design (Zar, 1974), determined if the numbers in each subadult age class were significantly different throughout each wintering season.

Results and Discussion

Population Numbers

Bald eagles winter on the Nooksack River between late October and late March (Fig. 2). The population gradually increases until January when the highest level is reached.

Peak counts of 91, 105, 96, and 118 were recorded for 1974-75, 1975-76, 1976-77, and 1977-78, respectively. Rapid departures occur shortly after mid-January. During both 1975-76 and 1976-77, there was a 60 percent reduction in the population two weeks after the peak counts. Other local populations include the Skagit River where 100 to 180 birds winter (Servheen and English, 1976). Peak counts of 148 and 35 for the southern Gulf Islands and San Juan Island, respectively, have been recorded; these populations, however, are suspected to be much larger (Hancock, 1964). We believe that our counts were conservative, especially with subadults since their plumages are less conspicuous than adults.

Age Class Dynamics

The proportion of subadults to adults was variable throughout both wintering seasons

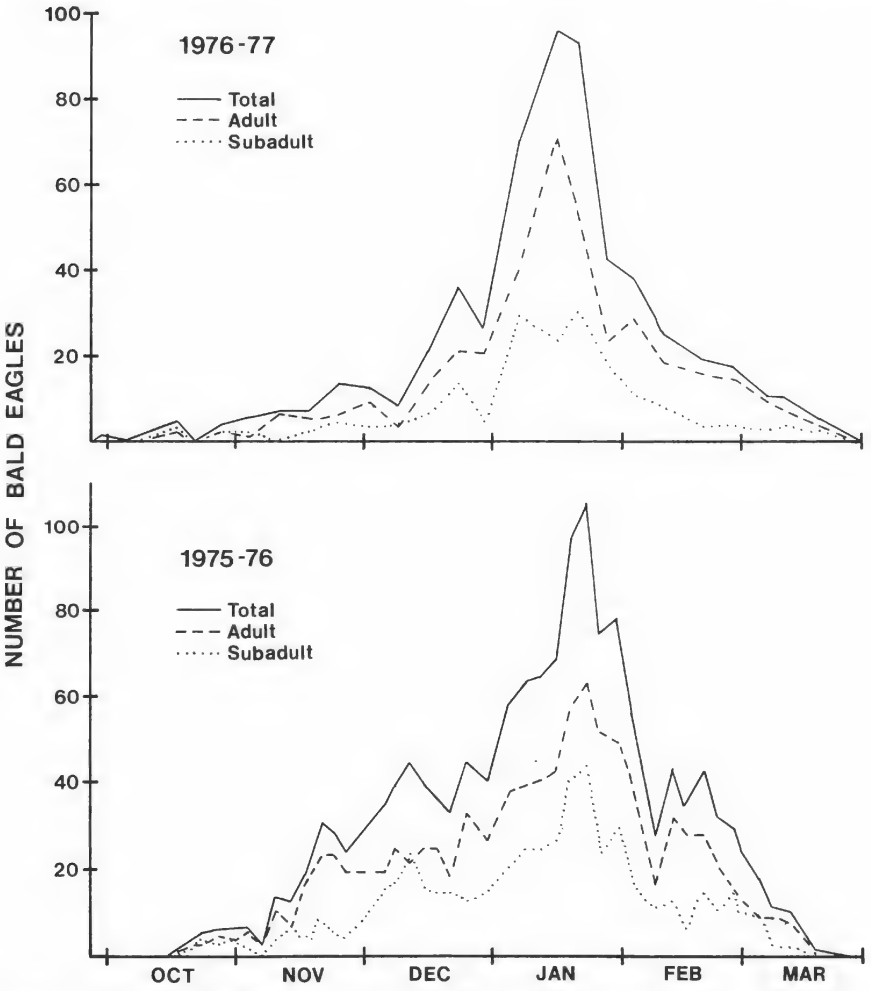

Figure 2. Number of bald eagles wintering in the Nooksack River study area during 1975-76 and 1976-77.

Figure 3. Percentage of subadult bald eagles, one through five years old, wintering in the Nooksack River study area during 1975-76 and 1976-77. Number of eagles is shown above each bar.

(Fig. 2). In 1975-76, adults generally arrived several weeks in advance of the subadults; this was not the case, however, in 1976-77. During both wintering seasons subadults formed a slightly lower proportion toward the end of the wintering period. Hancock (1964) and Servheen (1975) found a similar pattern of early adult arrival in the Pacific Northwest. Early subadult arrival, however, prevails in the interior contiguous states (Southern, 1963, 1964; Sprunt and Ligas, 1966; McClelland, 1973; and Shea, 1973).

Subadults constituted 36 and 32 percent of the population during 1975-76 and 1976-77, respectively. Subadult percentages ranging in the thirties were also found in Utah (Edwards, 1969), Montana (McClelland, 1973), and South Dakota (Steenhof, 1976), but proportions as low as 6 percent were recorded in Illinois (Southern, 1963). Percentages on San Juan Island were in the thirties (Hancock, 1964) and subadults made up 53 percent of the population on the Skagit River (Servheen, 1975). The higher percentage on the Skagit, just 40 miles southeast of our study area, may reflect the greater abundance of salmon carrion there. Subadult proportions tend to be higher where food is more plentiful (Stalmaster, 1976).

There was no significant ($P>0.05$) difference in the numbers in each subadult age class during both wintering seasons (Fig. 3) ($F=1.69$ for 1975-76, $df=4$, 164; $F=0.52$ for 1976-77, $df=4$, 100). During 1975-76, one year olds were generally the earliest subadult age class to arrive and the first to depart. Southern (1964) also found that first-year birds moved south earliest. Comparable age-class differences for subadults from 1975-76 to 1976-77 are not clearly evident with the available data.

Distribution and Density

Between 90 and 95 percent of the Nooksack River population winters inside the bound-

aries of the study area. Occasional sightings outside the study area were made on the south fork, upper north fork, and the mainstream. The greatest concentration of eagles is between Deming and Maple Falls on the north fork (Fig. 1). In this 11.5-mile stretch, 76 and 87 percent of the population aggregated during 1975-76 and 1976-77, respectively. Peak densities of seven birds per river mile were observed in this region. Dispersion along the river was distinctly greater than on the Skagit River. During 1974-75, 85 percent of the eagles on the Skagit were congregated in a 3.5-mile segment (Servheen, 1975).

Availability of salmon carcasses was the most important factor affecting eagle distribution. Other secondary food sources were also influential. Carcasses were widely spaced in the study area which explains the greater spread in eagle distribution in comparison to the Skagit River. Changes in distribution occurred throughout both seasons and reflected the amount of local salmon carrion. Mid-winter flooding was common and frequently washed away salmon carcasses which resulted in an attendant reduction in eagle numbers. Availability of suitable perch trees and the degree of human disturbance also affects distribution (Stalmaster and Newman, 1978).

Most eagles were distributed within 50 m of the river-channel during the day, but perching and roosting birds were observed throughout the river valley and adjacent ridges. Three communal night roosts, which accommodated up to 15 birds each, were located between 0.5 and 1.0 km from the river. All three roosts were in dense, coniferous forest which either bordered on clearings or had roost trees higher than the surrounding canopy.

Food Source

Chum salmon (*Oncorhynchus keta*) is the most important food source; however, coho (*O. kisutch*), pink (*O. gorbuscha*), and chinook (*O. tshawytscha*) are also utilized. Principal food sources on the Skagit River, southern Gulf Islands, and San Juan Island are salmon, dead domestic sheep, and feral rabbits (*Oryctolagus cuniculus*), respectively. Sockeye salmon (*O. nerka*) are relatively scarce and negligible as a food source. Pink salmon spawn and are available only during odd-numbered years. Chinook and pink spawn early in the wintering season, whereas chum and coho spawn later and over a longer period. Thus, availability of chum and coho is normally higher. All salmon were eaten as carrion. In addition, carrion of black-tailed deer (*Odocoileus hemionus*) and domestic cow were occasionally used as supplemental sources.

The presence of gravel and mud bars, side-channels, sloughs, and tributary deltas facilitates the deposition or beaching of salmon carcasses. These braided reaches have low water velocities which rarely wash carcasses away. Chum salmon select these areas for spawning beds, which explains their greater abundance as carrion.

Eagles prefer foraging in open areas. Carcasses on spawning grounds covered by a heavy canopy were seldom used. A decrease in utilization was also observed when snow covered carcasses. In addition, frozen carrion could not be eaten. Instead, submerged carcasses not frozen by low air temperatures were dragged to land and fed upon.

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Type Specimens of Birds Collected in Oregon

Abstract

Names of 44 avian taxa are based on specimens collected in Oregon. Of these, 3 species and 23 subspecies are currently recognized or should be considered distinct. The type locality and collecting data for each type-specimen and the present status of each taxon are indicated.

The identification of type specimens and information on the localities where they were collected are important in studies of taxonomy and nomenclature. This paper concerns the types and type localities of avian taxa based on specimens collected in Oregon. This information was obtained by examination of type specimens and critical scrutiny of all literature that concerns, in any way, the collection or description of such specimens. This project included consulting original descriptions, narratives, and journals, especially those of David Douglas, John K. Townsend, Thomas Nuttall, Titian R. Peale, Charles Wilkes, and John S. Newberry. These materials are in the Museum of Natural History Library, Smithsonian Institution.

Gabrielson and Jewett (1940:59-61) previously listed 35 birds that were described from specimens collected in Oregon. Their list included two names (*Falco communis*, var. *pealei* and *Phasianus columbianus*) that were actually based on specimens from Washington, and one form (*Zenaidura macroura caurina*) that possibly was collected in Washington. These three names are discussed at the end of this paper. Gabrielson and Jewett overlooked six previously proposed names and subsequent to their list six other forms have been described from specimens collected in Oregon, to bring the total to 44.

Each account begins with the name of the form as originally described, followed by its author and citation. The present status of the name is indicated when this name differs from that originally proposed. The concept of type used here follows that of Deignan (1961): a type may refer to a primary type (holotype, lectotype, or neotype) or to a syntype (often called a cotype). I have made no attempt to designate primary types. In most instances, when only one specimen is listed, it may be assumed to be the holotype unless otherwise stated. For names having syntypes with different collecting localities, the type locality of the name as generally recognized in the Fifth Edition of the A.O.U. (1957) Check-list will be that of the first specimen listed in the account.

Taxonomic decisions are based on comparisons of the types with other specimens and consultation of the literature. All type specimens were examined except those of *Phasianus columbianus* and *Ortyx picta*, which are no longer extant, and *Ortyx plumifera* and *"Poocaetes" grammineus affinis*. Names of three forms (*Baeolophus inornatus zaleptus*, *Oreortyx picta palmeri*, and *Otus asio brewsteri*) recognized in the A.O.U. (1957) Check-list are here considered synonyms; three forms (*Empidonax traillii*

adastus, *Cyanocitta stelleri paralia*, and *Hylochichla guttata oromela*) not recognized in the Check-list are here distinct, and one previously synonymized name (*Ortyx plumifera*) is resurrected. The taxonomy and nomenclature of all other forms in the following account follow the A.O.U. (1957) Check-list and its 32nd (A.O.U., 1973) and 33rd (A.O.U., 1976) supplements.

Astur atricapillus henshawi Nelson
Auk 1(1):166, April 1884.
now *Accipiter gentilis atricapillus* (Wilson, 1812)
USNM 79798. Adult female. Chewaucan Creek (southeast of Summer Lake, west of Lake Albert), Lake County, Oregon. 16 August 1878. Collected by H. W. Henshaw, original number 721. Explorations and Surveys West of the 100th Meridian.
USNM 85624. Adult male. Twelve miles E Big Tree, 6000 feet, Calaveras County, California. 19 June 1881. Collected by L. Belding.
USNM 85625. Same as 85624, but adult female collected 17 June 1881.
The syntypes listed above are those designated by Nelson (1887:141). I follow Ridgway (1884) in synonymizing *henshawi* with *A. g. atricapillus*.

Canace obscura var. *juliginosa* Ridgway
Forest and Stream 1(19):289, 18 December 1873.
now *Dendragapus obscurus juliginosus* (Ridgway, 1873)
USNM 4505 (not 11505). Adult male. Cascade Mountains near Mt. Hood, probably Hood River County, Oregon. 5-14 October 1855. Collected by C. D. Anderson for J. S. Newberry. Pacific Railroad Survey, Sacramento Valley to the Columbia River.
USNM 11826 and 11827. Adult female and immature (sex not indicated), respectively. Both specimens from the Chilliwack River, Fraser Valley Electoral District, British Columbia. The original description gave the locality as Chiloweyuck Depot, Washington Territory. 6 August 1858. Collected by C. B. R. Kennerly, original numbers 216 and 217, respectively. Northwestern Boundary Commission, 1858.

On the original label of the syntype from Oregon and in its entry in the USNM catalogue is the inscription "45°N." According to the maps and accompanying text on the route taken by Newberry (1857) and Anderson, 45°N latitude was crossed at a location southeast of Mt. Hood in Wasco County, a region on the east slope of the Cascade Mountains. This location is within the range of the race *sierrae* Chapman, 1904 (see Aldrich and Duvall, 1955). However, specimen 4505 is clearly a representative of the race *juliginosus* of the western slope of the Cascades. The Oregon type was probably collected on the western slope of the Cascades while the survey party was making its way to the Willamette Valley.

The original description of *juliginosus* has erroneously been regarded as having been published in the December 1873 issue of the Bulletin of the Essex Institute (Baird and Ridgway, 1873 [=1874]) (e.g. Peters, 1934; Helmayr and Conover, 1942; Ridgway and Friedmann, 1946; A.O.U. 1957). The name was first used with a description published on 18 December 1873 by Ridgway (1873). A second, more detailed description (Ridgway, 1874) was published on 3 January 1874, and a third was provided by Baird and Ridgway (published in February 1874, not December 1873, footnote, p. 201) in which the three syntypes listed here were included in an elaborated version of the earlier descriptions.

Bonasa umbellus affinis Aldrich and Friedmann
Condor 45(3):97, 24 May 1943.
USNM 95021. Adult male, gray phase. Fort Klamath, Klamath County, Oregon. 28 October 1882. Collected by C. E. Bendire, original number 254.

Centrocercus urophasianus phaios Aldrich
Proc. Biol. Soc. Washington 59(26):129, 25 October 1946
USNM 259861. Adult male. Fremont, Lake County, Oregon. 21 August 1914. Collected by L. J. Goldman, original number 106.

Lophortyx californica orecta Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):2, 19 September 1932.
now *Lophortyx californicus californicus* (Shaw, 1798)
CMNH 15001. Adult male. Nine miles S. Adel, mouth of Twenty Mile Creek, Warner Valley, Lake County, Oregon. 17 October 1930. Collected by A. Walker, original number 3593.
The putative race *orecta* from central-southern Oregon is not separable from the nominate form (van Rossem, 1939; Miller, 1941; Browning, 1974b).

Ortyx picta Douglas
Philosophical Magazine, new ser. 5(25):74, January 1829.

now *Oreortyx pictus pictus* (Douglas, 1829)
Type not extant. Type locality: junction of the Willamette and Santiam rivers, Linn County, Oregon. November 1826. Collected by D. Douglas.

The type-locality of *Ortyx picta* as given was designated (Browning, 1977) on the basis of the writings of David Douglas. The nominate form previously was considered to be the pale race east of the Cascade Mountains, and *O. p. palmeri* the dark western race (Oberholser, 1923). Since *pictus* is based on specimens of the dark form, the name palmeri becomes a synonym of *pictus*. The pale form is *O. p. plumiferus*.

Ortyx plumifera Gould
Icocnes Avium I, pl. 9, p. 1, August 1837.
now *Oreortyx pictus plumiferus* (Gould, 1837)
BM 1855.12.19.30. First year bird, sex unknown. Wasco County, Oregon. Found in the baggage of D. Douglas.

The lectotype and two syntypes were probably obtained by David Douglas from a hunter at Ft. Vancouver (=Vancouver, Washington) who collected the holotype and one syntype east of the Cascade Mountains in Oregon and the other syntype (=*O. p. pictus*) west of the Cascades (Browning, 1977).

Oreortyx picta palmeri Oberholser
Auk 40(1):84, 10 January 1923.
now *Oreortyx pictus pictus* (Douglas, 1829)
USNM 140847. Adult male. Yaquina, Lincoln County, Oregon. 7 December 1893. Collected by C. P. Streator.

Specimens from west of the Cascade Mountains are referable to the dark nominate race (Browning, 1977).

Otus asio brewsteri Ridgway
Birds of North and Middle America 6:685 (in key), 700, 8 April 1914.
now *Otus asio kennicottii* (Elliot, 1867)
USNM 120014. Adult male. Salem, Marion County, Oregon. 17 February 1891. Collected by C. T. Cooke, original number 974.

I follow Marshall (1967) in considering *brewsteri* a synonym of *kennicottii*.

Phalaenoptilus nuttallii nyctophilus Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):2, 19 September 1932.
now *Phalaenoptilus nuttallii nuttallii* (Audubon, 1844)
CMNH 15002. Adult female. Twenty miles NE Adel, northern end of Warner Valley near site of Old Fort Warner, Hart Mountain, Lake County, Oregon. 9 August 1930. Collected by A. Walker, original number 3030.

Birds ascribed to *nyctophilus* are intermediate between *P. n. californicus* and *nuttallii*, but are closer to the latter race (Miller, 1941).

Picus williamsoni Newberry
Rep. Expl. Surv. R. R. Pacific 6(4):89, pl. 34 (upper figure), 1857.
now *Sphyrapicus thyroideus thyroideus* (Cassin, 1851)
USNM 9344. Adult male. "In the pine forest bordering upper Klamath Lake on the east," Klamath County, Oregon. 23 August 1855. Collected by J. S. Newberry.

Henshaw (1874) synonymized *Picus williamsoni* with *Sphyrapicus thyroideus*.

Picoides arcticus tenuirostris Bangs
Auk 17(2):131, April 1900.
now *Picoides arcticus* (Swainson, 1832)
MCZ 219576. Adult male. Fort Klamath, Klamath County, Oregon. 13 December 1886. Collected by J. C. Merrill.

Picoides arcticus is monotypic (Ridgway, 1914).

Tyrannus tyrannus hespericola Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):3, 19 September 1932.
now *Tyrannus tyrannus* (Linnaeus, 1758)
CMNH 15004. Adult male. Nine miles S. Adel, mouth of Twenty Mile Creek, Warner Valley, Lake County, Oregon. 21 May 1930. Collected by A. Walker, original number 2378.

Tyrannus tyrannus is monotypic (Zimmer, 1937; Miller, 1941).

Empidonax traillii adastus Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):3, 19 September 1932.
CMNH 15003. Adult Male. Twenty miles NE Adel, northern end of Warner Valley, Hart Mountain, Lake County, Oregon. 13 June 1930. Collected by A. Walker, original number 2566.

Empidonax t. adastus is not recognized in the A.O.U. (1957) Check-list but this dark form, breeding in the northern Great Basin, is considered distinct by several authorities (e.g. Phillips, 1948; Aldrich, 1951; Aldrich *in* Jewett *et al.*, 1953; Phillips *in* Phillips *et al.*, 1964; Wetmore, 1972). The A.O.U. (1973) included the range of *adastus* in that of *brewsteri*.

Otocoris alpestris merrilli Dwight
Auk 7(2):153, April 1890.
now *Eremophila alpestris merrilli* (Dwight, 1890)
MCZ 218882. Adult female. Fort Klamath, Klamath County, Oregon. 26 October 1887. Collected by J. C. Merrill.
MCZ 219516. Same as above but adult male collected on 1 July 1887.
MCZ 219524. Same as 219516 but juvenile male.
MCZ 219538. Same as 218882 but adult female collected on 23 May 1887.

Otocoris alpestris lamprochroma Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):4, 19 September 1932.
now *Eremophila alpestris lamprochroma* (Oberholser, 1932)
CMNH 15005. Adult male. Twenty miles NE Adel, Spanish Lake, E base Hart Mountain, northern end Warner Valley, Lake County, Oregon. 12 June 1930. Collected by A. Walker, original number 2557.

The characters distinguishing *lamprochroma* from *merrilli* are minor. Aldrich (*in* Jewett *et al.*, 1953) found it difficult to separate specimens of the two races from southeastern Washington. I find it difficult to identify specimens from northeastern Oregon, where *merrilli* and *lamprochroma* interbreed (Behle, 1942). Because of the minor differences between *merrilli* and *lamprochroma* and the broad zone intergradation between these races, I consider the utility of recognizing *lamprochroma* as questionable.

Stelgidopteryx ruficollis aphractus Oberholser
Sci. Publ. Cleveland Mus. Hist. 4(1):5, 19 September 1932.
now *Stelgidopteryx ruficollis serripennis* (Audubon, 1838)
CMNH 15006. Adult female. Nine miles S. Adel, Twenty Mile Creek. Warner Valley, Lake County, Oregon. 23 April 1930. Collected by A. Walker, original number 2151.
Miller (1941) synonymized *aphractus* with *serripennis.*

Petrochelido albifrons aprophata Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):6, 19 September 1932.
now *Petrochelidon pyrrhonota hypopolia* Oberholser, 1919
CMNH 15007. Adult male. Nine miles S. Adel, south of Twenty Mile Creek, Warner Valley, Lake County, Oregon. 19 June 1930. Collected by A. Walker, original number 2611.

Specimens from the Warner Valley are intergrades between nominate *pyrrhonota* and *hypopolia* but more closely resemble the latter race (van Rossem, 1936; Miller, 1941; Behle, 1976).

Cyanocitta stelleri paralia Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):7, 19 September 1932.
CMNH 15018. Adult male. Nine miles SE Tillamook, Pleasant Valley, Tillamook County, Oregon. 14 January 1930. Collected by A. Walker, original number 1428.

Oberholser (1932) applied the name *paralia* to the birds breeding from southwestern British Columbia west of the Cascade Mountains south to western Oregon. This race was described as being smaller and paler than *C. s. stelleri* of Vancouver Island and larger and darker than *carbonacea* of west-central California. I follow Stevenson (1934) and Aldrich (*in* Jewett *et al.*, 1953) in recognizing *paralia.* The A.O.U. (1957) does not recognize *paralia* and its range is included in nominate *stelleri.*

Cyanocitta stelleri syncolla Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):6, 19 September 1932.
now *Cyanocitta steller frontalis* (Ridgway, 1873)
CMNH 15017. Adult female. Fourteen miles SW Adel, 6400 feet, Barley Camp, Warner Mountains, Lake County, Oregon. 10 July 1930. Collected by A. Walker, original number 2794.
Stevenson (1934) and Miller (1941) synonymized *syncolla* with *frontalis.*

Aphelocoma coerulescens immanis Grinnell
Auk 18(2):188, April 1901.
MVZ 33789. Adult male. Scio, Linn County, Oregon. 9 January 1901. Collected by A. G. Prill, number 4582 of J. Grinnell's collection.

Aphelocoma coerulescens caurina Pitelka
Univ. California Publ. Zoo. 50(3):225, 20 July 1951.
MVZ 97715. Adult male. One mile E. Wedderburn, 50 feet, Curry County, Oregon. 10 October 1947. Collected by W. C. Russell, original number 10663.
The present use of the name *A. c. oocleptica* follows that of the A.O.U. (1957).

C [*orvus*]. *americanus hesperis* Ridgway
Manual of North American Birds, p. 362, September 1887.
now *Corvus brachyrhynchos hesperis* Ridgway, 1887

USNM 94976. Adult female. Fort Klamath, Klamath County, Oregon. 26 March 1883. Collected by C. E. Bendire, original number 453.
USNM 94977. Same as above but adult male, collected on 8 April 1883; original number, 467.

A type and type locality for *hesperis* was not designated in the original description but Ridgway (1904) later implied that the type locality should be restricted to Ft. Klamath. According to Deignan (1961), the two specimens listed above are the only remaining specimens from the original series.

Baeolophus inornatus sequestratus Grinnell and Swarth
Univ. California Publ. Zool. 30(5):166, 16 September 1926.
now *Parus inornatus sequestratus* (Grinnel and Swarth, 1926)
MVZ 46163. Adult male, Eagle Point, Jackson County, Oregon. 26 November 1925. Collected by W. Sherwood.

Baeolophus inornatus zaleptus Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):7, 19 September 1932.
now *Parus inornatus ridgwayi* Richmond, 1902
CHNM 15008. Adult Female. Nine miles S. Adel, Twenty Mile Creek, rim of Warner Valley northwest of Jacobs Ranch, Lake County, Oregon. 3 May 1930. Collected by A. Walker, original number 2231.

Phillips (*in* Phillips *et al.*, 1964) applied the name *ridgwayi* to all gray populations found breeding in the Great Basin, including *zaleptus* (*contra* Linsdale, 1938; Miller, 1941; A.O.U. 1957.)

Chamaea fasciata phaea Osgood
Proc. Biol. Soc. Washington 13:42, 29 May 1899.
USNM 164256. Adult male. Newport, Lincoln County, Oregon. 14 March 1899. Collected by B. J. Bretherton, original number 2405.

Thryomanes bewickii atrestus Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):8, 19 September 1932.
CMNH 15009. Adult male. Nine miles S. Adel, mouth of Twenty Mile Creek, Warner Valley, Lake County, Oregon. 17 October 1930. Collected by A. Walker, original number 3595.

Hylochichla buttata oromela Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):8, 19 September 1932.
now *Catharus guttatus oromelus* (Oberholser, 1932)
CMNH 15010. Adult male. Fifteen miles NE Lakeview, north base of Crook Peak, Warner Mountains, Lake County, Oregon. 28 August 1930. Collected by A. Walker, original number 3187.

I follow Phillips (1962) and Aldrich (1968) in recognizing *oromelus* for the birds breeding from central northern California northward in the Cascade Mountains to central British Columbia.

Ptilogonys townsendi Audubon
Birds of America (folio) 4(84), pl. 419, fig. 2, 1838.
now *Myadestes townsendi townsendi* (Audubon, 1838)
USNM 2922. Adult female. Astoria, Clatsop County, Oregon. Collected by W. Brotchie.

The specimen label reads "Columbia River," but according to Townsend (1839) the specimen was collected near Ft. George (=Astoria).

Vireo huttoni obscurus Anthony
Zoe 1(10):307. December 1890.
now *Vireo huttoni huttoni* Cassin, 1851
CM 16981. Adult female. Beaverton, Washington County, Oregon. 20 March 1890. In the Collection of A. W. Anthony as number 2671.

This specimen, like many from the Anthony collection, is badly soiled, a condition which may have led Anthony to name a dark race. Grinnell (1922) and Oberholser (1922) synonymized the name *obscurus* with nominate *huttoni.*

Vireosylva gilva leucopolia Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):9. 19 September 1932.
now *Vireo gilvus leucopolius* (Oberholser, 1932)
CMNH 15011. Adult male. Fourteen miles SW Adel, 6400 feet, Barley Camp, Warner Mountains, Lake County, Oregon. 15 July 1930. Collected by A. Walker, original number 2840.

S [*ylvia*] *nigrescens* J. K. Townsend
Journ. Acad. Nat. Sci. Philadelphia 7(2):191, November 1837.
now *Dendroica nigrescens* (Townsend, 1837).
USNM 1908. Adult male. Vicinity of Fort Williams (Portland), Multnomah County, Oregon. 16 June 1835. Collected by J. K. Townsend.

USNM 2915. Same as above but collected on 14 May 1835.
The specimen label of 1908 reads "Columbia River," but according to Townsend (1839) the bird was taken near Ft. Williams.

Geothlypis trichas oregonicolo Oberholser
Descriptions of new races of *Geothlypis trichas* (Linnaeus), privately published, Cleveland, p. 3, 20 January 1948.
now *Geothlypis trichas occidentalis* Brewster, 1883
CMNH 16181. Adult male. Six miles S. Adel, Warner Valley, Lake County, Oregon. 16 June 1930. Collected by A. Walker, original number 2582.
I follow Behle (1950) who synonymized *oregonicola* with *occidentalis*.

Euphagus cyanocephalus aliastus Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):9, 19 September 1932.
now *Euphagus cyanocephalus* (Wagler, 1829)
CMNH 15012. Adult female. Nine miles S. Adel, Twenty Mile Creek, Warner Valley, Lake County, Oregon. 2 May 1930. Collected by A. Walker, original number 2230.
The variation described by Oberholser (1932) is independent of geographic variation (Miller, 1941).

Leucosticte tephrocotis wallowa A. H. Miller
Condor 41(1):34, 17 January 1939.
MVZ 73998. Adult male. Eighteen miles S, 2 miles E. Lostine, 8800 feet, north face of Elkhorn Peak, Wallowa Mountains, Wallowa County, Oregon. 14 July 1938. Collected by A. H. Miller, original number 3263.

Loxia curvirostra bendirei Ridgway
Proc. Biol. Soc. Washington 2:101, 28 April 1884.
USNM 94881. Adult male. Fort Klamath, Klamath County, Oregon. 8 January 1883. Collected by C. E. Bendire, original number 390.
USNM 94892. Same as above but adult female collected on 5 December 1882, original number 314.
A type was not designated in the original description, but the two specimens listed above were thus marked by Ridgway (*fide* Deignan, 1961).

Pipilo fuscus bullatus Grinnell and Swarth
Univ. California Publ. Zool. 21(18):431, 6 April 1926.
MVZ 46578. Adult male. Eagle Point, Jackson County, Oregon. 9 January 1926. Collected by W. E. Sherwood.

Oberholseria chlorura zapolia Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):10, 19 September 1932.
now *Pipilo chlorurus* (Audubon 1839)
CMNH 15013. Adult male. Twenty miles NE Adel, northern end of Warner Valley, Hart Mountain, Lake County, Oregon. 9 June 1930. Collected by A. Walker, original number 2515.
Pipilo chlorura is monotypic (Miller, 1941; A.O.U., 1957; Paynter, 1970).

Pooecetes gramineus definitus Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):11, 19 September 1932.
now *Pooecetes gramineus confinis* Baird, 1858
CMNH 15014. Adult male. Nine miles S. Adel, Twenty Mile Creek, Warner Valley, Lake County, Oregon. 3 May 1930. Collected by A. Walker, original number 2236.
I follow Miller (1941) and Phillips (1964) who synonymized *definitus* with *confinis*.

Poocaetes gramineus affinis G. S. Miller
Auk 5(4):404, October 1888.
now *Pooecetes gramineus affinis* Miller, 1888
BM 1906.12.7.3737. Adult male. Salem, Marion County, Oregon. 29 May 1887. Collected by G. S. Miller.
The holotype was listed in the original description as having the number 2503 of Miller's collection. The specimen was not received by the British Museum (Natural History) until 1937 but was given the registration number of the original collection (Warren and Harrison, 1971).

Chondestes grammacus actitus Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):12, 19 September 1932.
now *Chondestes grammacus strigatus* Swainson, 1827
CMNH 15015. Adult male. Nine miles S. Adel, mouth of Twenty Mile Creek, Warner Valley, Lake County, Oregon. 26 May 1930. Collected by A. Walker, original number 2411.
The race *actitus* is not separable from *strigatus* (see Miller, 1941).

Junco hyemalis simillima Phillips
Annals Inst. Biol. Mexico 32(1, 2):376, 30 March 1962.
now *Junco hyemalis simillimus* Phillips, 1962
DMNH 18515. Immature male. Pringle Falls, 4245 feet, Experiment Station (Deschutes National Forest), Deschutes County, Oregon. 16 September 1953. Collected by S. G. Jewett, original number 14034.
DMNH 18516. Same as above but adult female collected on 15 September 1953, original number 14032.
DMNH 18517. Same as 18515 but original number 14033.
DMNH 18518. Same as 18515 but adult female collected on 18 September 1953, original number 14043.

Phillips (1962) showed that the type of *shufeldti* Coale, 1887, was a migrant of the race *montanus* Ridgway, 1898 (*sensu* A.O.U., 1957) and renamed the northwestern race *simillimus* (see Browning, 1974a).

Zonotrichia leucophrys oriantha Oberholser
Sci. Publ. Cleveland Mus. Nat. Hist. 4(1):12, 19 September 1932.
CMNH 15016. Adult male. Fourteen miles SW Adel, 6400 feet, Barley Camp, Warner Mountains, Lake County, Oregon. 8 July 1930. Collected by A. Walker, original number 2771.

Banks (1964) considered *oriantha* to be a synonym of nominate *leucophrys*. I prefer to follow Miller (1941) and Godfrey (1965) in recognizing *oriantha* with a breeding range from south-central Oregon southward to central eastern California (Oberholser, 1932, 1974; Browning 1974a).

Melospiza cinerea phaea W. K. Fisher
Condor 4(2):36, March 1902.
now *Melospiza melodia morphna* Oberholser, 1899
MVZ 35954. Adult male. Mouth of Umpqua River, Gardiner, Douglas County, Oregon. 1 December 1901. Collected by E. Heller (for J.G.), original number 4974.

"J. G." on the original label refers to Joseph Grinnell. I follow Swarth (1923) in considering the name *phaea* as a synonym of *morphna*.

The following three accounts include taxa that were based on specimens from other than Oregon:

Falco communis, var. *pealei* Baird and Ridgway
In Baird and Ridgway, Bull. Essex Inst. 5:201, December 1873 [=February 1874].
now *Falco peregrinus pealei* Baird and Ridgway, 1873 [1874]
USNM 12022. Immature female. Puget Sound, Washington. U.S. Exploring Expedition (1838-1842).
USNM 45814. Immature (not adult) female. Sitka, Baranof, Alaska, May 1866. Collected by F. Bischoff.

Specimen 12022 was collected at Puget Sound (Peale, 1848), not in Oregon (*contra* Gabrielson and Jewett, 1940). Deignan (1961) stated that the location "Oregon" was taken from the old exhibition label still affixed to the specimen. The original description appeared in the December 1873 issue of the Bulletin of the Essex Institute, which was not issued until February 1874.

Phasianus columbianus Ord
In Gutherie, Geogr., 2nd Amer. ed., p. 317, 1815.
now *Pedioecetes phasianellus columbianus* (Ord, 1815)
Type not extant. Based on the Prairie Hen of Lewis and Clark, Exped. Rocky Mtns., vol. 2:180-182. Type locality: Great Plains of the Columbia River near the mouth of the Snake River, Washington.

Gabrielson and Jewett (1940) incorrectly considered the type locality of this form as the region between the mouths of the Deschutes and Snake rivers, Oregon. The type locality was restricted by Hall (1933) as indicated above.

Zenaidura macroura caurina Ridgway
Birds of North and Middle America 7:348 (footnote), 5 May 1916.
now *Zenaida macroura marginella* (Woodhouse, 1852)
USNM 12540 (not 22540 as was listed in the description). On the Columbia River, probably not far upstream from the Pacific coast (Oregon or Washington). Collected by T. R. Peale. U.S. Exploring Expedition (1838-1842).

Gabrielson and Jewett (1940) reported the type as having been collected in Oregon, but Aldrich and Duvall (1958) restricted the type locality of *caurina* as stated above and were unable to more definitely establish the collecting locality or date of the type. The name Oregon, affixed to a label removed from the base on which the type was mounted, in Peale's time was sometimes applied to regions other than as currently recognized, and the type may have been collected in

Oregon or Washington. The number 451 on the aforementioned label, indicated as the original number by Deignan (1961), refers to a species number in a list of birds by Baird (1858). Peters (1937) and Aldrich and Duvall (1958) synonymized the name *caurina* with *marginella.*

Acknowledgments

For permitting me to examine specimens under their care and for providing information, I am indebted to the curators of the following collections now holding type specimens reported herein: British Museum (Natural History) (BM), Carnegie Museum of Natural History (CM), Cleveland Museum of Natural History (CMNH), Delaware Museum of Natural History (DMNH), Museum of Comparative Zoology (MCZ), Museum of Vertebrate Zoology (MVZ), and the National Museum of Natural History (USNM). I thank the curators of the following collections for providing me the opportunity to examine additional comparative material: American Museum of Natural History, Oregon State University Museum of Natural History, Southern Oregon College, and University of Puget Sound Museum of Natural History. I am grateful to John W. Aldrich, Joe T. Marshall, and Storrs L. Olson for reading an early version of this paper, and Richard C. Banks for his helpful criticism of a later draft of the paper. I am indebted to an unknown reviewer of the manuscript.

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Joint Analysis of the Magnesite Belt of Stevens County, Washington

Abstract

The magnesite belt is a zone of closely folded metasedimentary and mafic intrusive rocks of widely different ages forming the west limb of an anticlinorium plunging north to north-northeast. An early phase of folding produced upright and inclined folds plunging north to north-northeast; a second phase produced west-plunging minor crenulations in the first stage foliation and gentle warps in the older folds. The folded rocks are intruded by the Cretaceous (100 m.y.) granitic Loon Lake batholith. Both metasedimentary and igneous rocks are strongly jointed. Attitudes of more than 2000 joints in the 500 square km area reveal that most joints fall into one of seven joint sets. The average strike and dip of each of these sets is as follows: Set A stk due N, dip E, variable; set B stk NE to N to NW, dip S, variable; set C stk N78E, dip 80SE; set D stk N73W, dip 88SW; set E stk N20W to N33W, dip 65NE to 75NE; set F stk N20E, dip 45SE; set G stk N30E, dip 90. Sets A, B, and C are present in the metasedimentary rocks; sets D and E are present in both the granitic and metasedimentary rocks; sets F and G are present only in the granitic rocks.

Sets A and B are related to the folds and are the oldest (Jurassic?) in the area. Set C is younger than the folds and older than the Cretaceous batholith. Joint sets D, E, and F were formed shortly after the intrusion of the Loon Lake batholith and about contemporaneously with the magnesite veins. Set G is the youngest set, having formed in late Cretaceous to Eocene time, probably contemporaneously with the emplacement of quartz veins, rhyodacite dikes, and the San Poil volcanic rocks.

Introduction

The magnesite belt of northeastern Washington (Fig. 1) is at the southwest extremity of the Kootenay Arc. It contains large deposits of magnesite as well as base metal deposits of considerable economic interest. Major base metal deposits occur within similar strata in neighboring British Columbia.

The purpose of this report is to describe the systematic joints of the belt and to establish the relative ages of joints, fold elements, and joint-controlled base metal and magnesite mineralization.

Geologic Setting

The magnesite belt is a zone of closely folded metasedimentary, volcanic and mafic intrusive rocks of widely different ages (Fig. 2). The metasedimentary rocks, which belong to the Deer Trail Group of Late PreCambrian age, are fine-grained clastics, quartzite and dolomite with an aggregate thickness greater than 3000 m. To the west of the

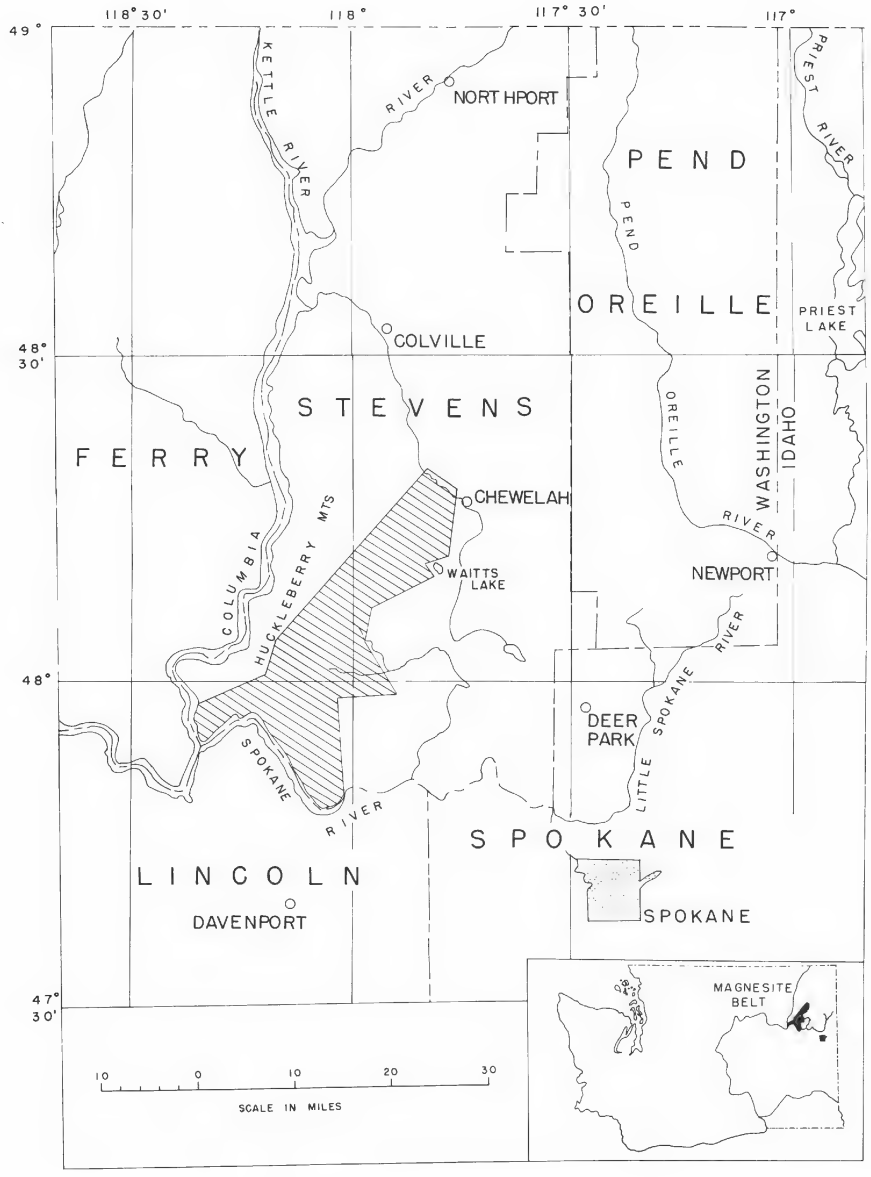


Figure 1. Index map of northeastern Washington showing location of report area.

belt the rocks of the Deer Trail Group are unconformably overlain by the Addy Quartzite of Early Cambrian age. Still farther west, in the Hunters quadrangle, is the Old Dominion Limestone of Cambrian age (Weaver, 1920), above which is a sequence of chert, limestone, and slate of Paleozoic age. Farthest west are Late Paleozoic and Early Mesozoic interbedded chert, slate, greenstone, limestone, grawacke and impure quartzite with beds of black slate of the Covada Group.

Intrusive and extrusive rocks range in age from PreCambrian to Tertiary. Dikes and sills of greenstone occur within the Deer Trail Group throughout the region, but are

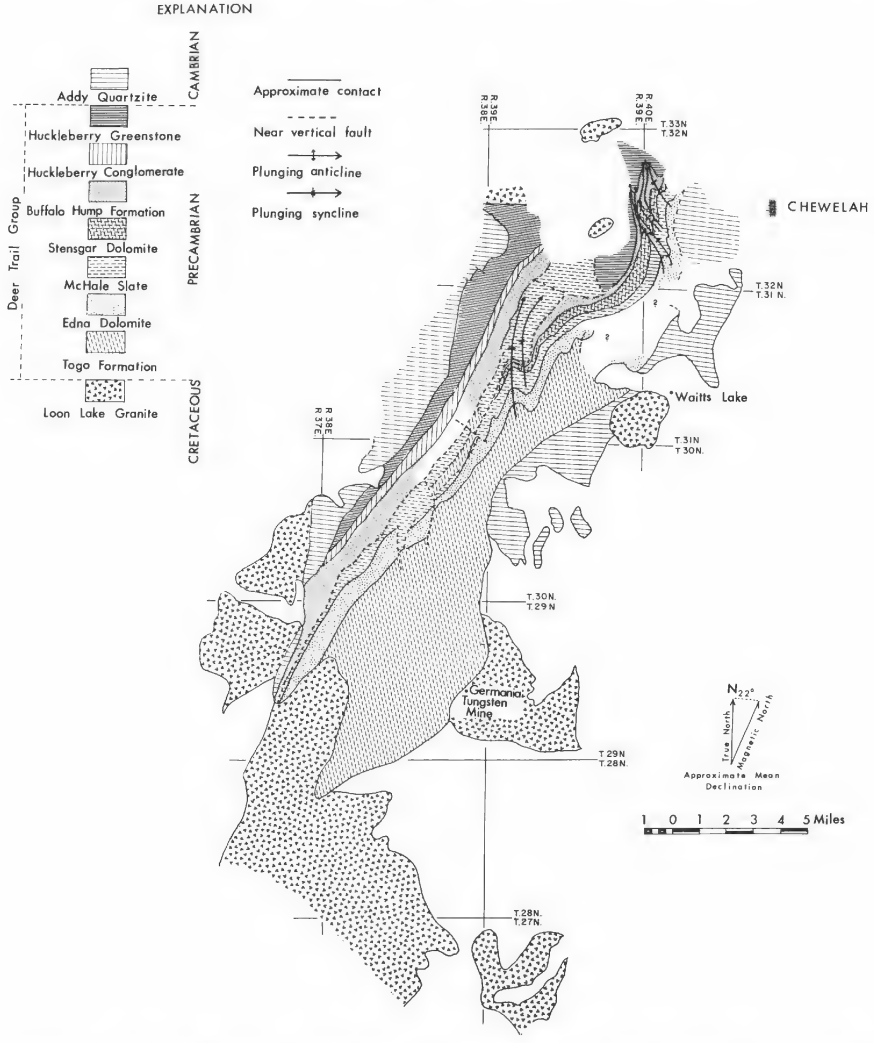


Figure 2. Generalized map of the magnesite belt, northeastern Washington. (Slightly modified from Campbell and Loofbourow, 1962, Geology of the magnesite belt of Stevens County, Washington: U.S. Geol. Survey Bull. 1142-F, Plate 1).

not known to penetrate the Huckleberry Greenstone or younger rocks; hence, they are thought to be feeders for the pillow basalts of the Huckleberry Greenstone.

The Loon Lake batholith in the southern portion of the map area consists mainly of granodiorite, porphyritic quartz monzonite, and equigranular quartz monzonite. Aplite, pegmatite, granite porphyry, and lamprophyre dikes cut the batholith. The granitic dikes, stocks, and the batholith are considered to be related because of their similar composition and lack of features attributable to intensive regional metamorphism. They cut the folded PreCambrian rocks and are themselves overlain and cut by rocks of Tertiary age. The age of the Loon Lake batholith is approximately 100 m.y. (Becraft and Weis, 1963) based upon lead alpha ages of zircon from the porphyritic quartz monzonite and grandiorite.

Andesite flows of the San Poil Volcanics and associated tuffs, sandstone, and carbonaceous shales overlie the Deer Trail Group and the Loon Lake batholith unconformably in the southwestern part of the area. Porphyritic rhyodacite dikes of the San Poil Volcanics cut the granodiorite and quartz monzonite.

The rocks of the magnesite belt display one type of metamorphism associated with folding, another associated with the greenstone dikes and sills, and a third associated with the granitic intrusives. Regional metamorphism accompanying folding and development of cleavage and schistosity has affected all sedimentary rocks of the belt. Minerals formed during metamorphism, including sericite, talc, chlorite, and actinolite, categorize the metamorphic facies as greenschist (Turner, 1968).

Local thermal metamorphism associated with the intrusion of the greenstone dikes and sills has recrystallized the Edna Dolomite to a coarse marble (Campbell and Loofoburow, 1962). The highest grade of metamorphism (hornfels) seems only to be present in narrow zones around the granite bodies. The principal neocrystallization minerals are biotite and cordierite.

Folds, Foliation, and Lineation

The area has been affected by at least two periods of folding. The first produced a north to north-northeastward plunging anticlinorium of which only the west limb is now present. Most first stage folds, expressed by compositional layering and bedding, are upright to steeply inclined and northerly plunging on this limb. They are flexural-slip folds which vary in wave length from a centimeter to several hundred meters. Folds of large amplitude and wave lengths have been developed in the incompetent layers. The slaty and argillic units involved in the folding display pronounced axial plane foliation. Crenulations in this foliation are parallel to the major fold axes suggesting that they were developed late during the first deformation. The second period of folding produced gentle warps in the older folds and widespread small scale crenulations, crenulation cleavage, and slip cleavage in the first stage axial plane foliation. This second stage warping and crenulation plunges very steeply west at a high angle to the first stage folds and foliation.

Lineation (L1) developed during the first stage deformation takes the form of pebble elongation in the Huckleberry Conglomerate and Addy Quartzite, pillow elongation in the Huckleberry Greenstone, boudins in the Edna Dolomite, and intersections of bedding and axial plane foliation. Lineation (L2) developed during the second deformation is expressed by axial lines or hinges of crenulations and by the intersection of crenulation cleavage or slip cleavage with the first stage axial plane foliation.

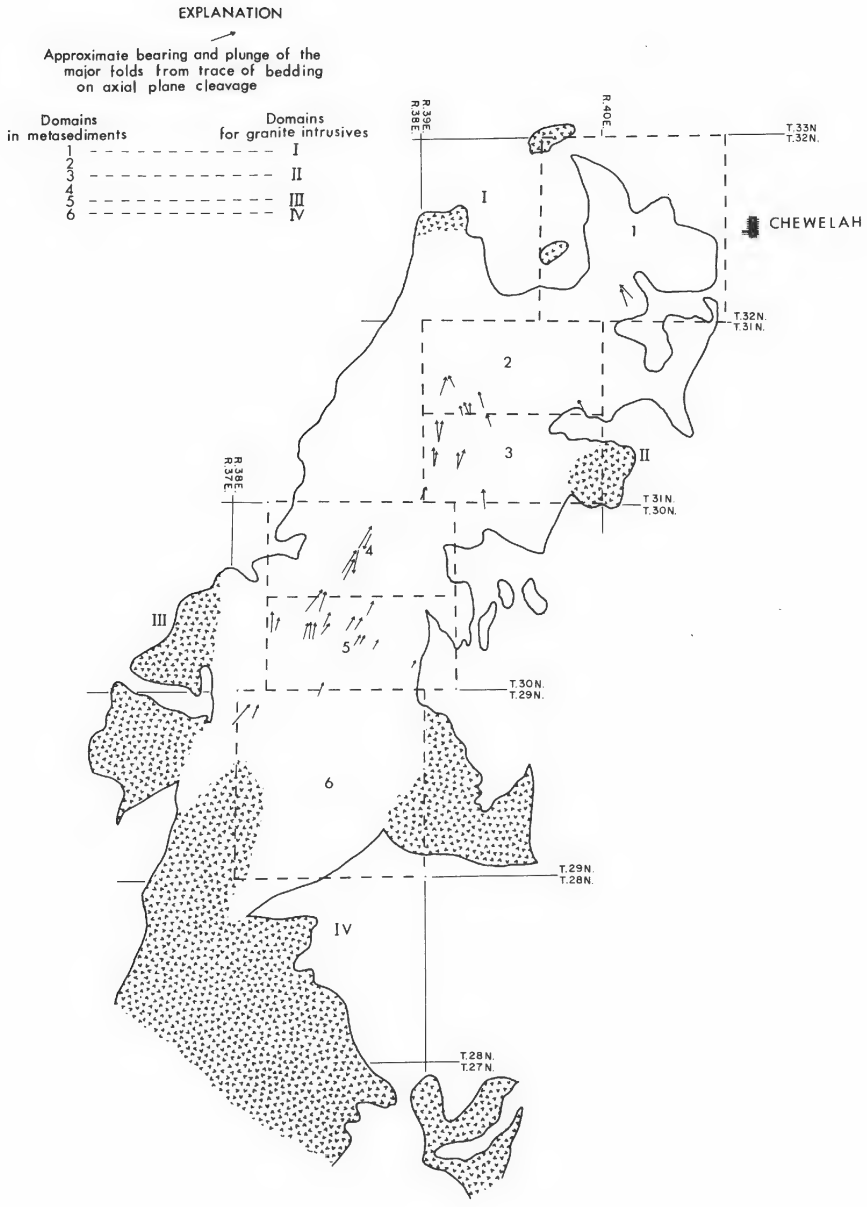


Figure 3. Map showing the location of six fold domains (number 1-6) within the metasedimentary rocks of the report area. These were selected on the basis of homogeneity of trend of trace of bedding on axial plane foliation. Also shown are four joint domains (designated I-IV) in plutonic rocks.

Faults

At least two generations of faults are present within the area. Two major nearly vertical longitudinal faults run for almost the entire length of the magnesite belt. One of these faults terminates to the south against the Loon Lake batholith. They exhibit vertical displacement in which the east side is usually down. Major transverse vertical faults displace the longitudinal faults and folds. Minor right lateral transverse faults strike N60W to N80W and dip steeply south. These minor faults are younger than all other structures in the magnesite belt for they displace both dikes and quartz veins in the granitic rocks.

Mesoscopic Fabric and Structure Analysis

Fold analysis compares and correlates fold geometry with joint patterns. One hundred and eighty lineations (L1 and L2) and poles to 845 bedding planes, 350 axial plane foliation surfaces, and 1074 joint surfaces were plotted and contoured on Schmidt equal-area projection nets (Figs. 4, 5, and 6). In order to compare joint patterns to fold trends, the report area was first divided into six domains, as illustrated in Figure 3. Each domain is a structurally homogeneous area to the extent that the fold trends are approximately the same throughout any given domain. That is, folding in each domain is almost cylindrical and is characterized on the stereoplot by a single great circle and by a common βS_0 axis.

From a combination of the βS_0, B_1 axis, and L1 lineations the local structural grain was calculated for each domain. A continuous change in the style and orientation of both the folds and fold-related structures is apparent from domain 1 to domain 6 (Figs. 4 and 5). The major and minor folds, lineations, and strike of axial plane foliation gradually change their orientation from N30W in domain 1 to N24E in domain 6. The general change in strike of the axial plane foliation is accompanied by a steepening in dip from 40W in domain 1 to 80E in domain 5.

Joint Analysis

Accumulation of Joint Data

Attitudes of 2000 joints were recorded from over 250 stations where joints were well exposed. Generally, only outcrops that exposed a minimum of four parallel joint surfaces were used. Irregular fractures without a consistent orientation were avoided. Usually one representative attitude was taken for four approximately parallel joints. Less often attitudes were determined for each of four joints and an average calculated and entered as one recording. The 2000 joint attitudes recorded represent roughly the averages of 8000 joint surfaces. The number of joints recorded at a station ranged from one to over one hundred, but averaged about eight.

The density, persistence, regularity, general jointing aspect, nature of the joint surface, and nature of mineral filling were recorded for each joint. Orientation of outcrop, bed thickness, lithology and presence of other structures were recorded also. Joint descriptions are given in the Appendix.

Poles to joint surfaces were plotted on Schmidt equal-area nets and contoured at intervals of 2, 5, 10 percent, etc. Joints in the metasedimentary rocks were plotted on six nets which represent the six domains of the entire area.

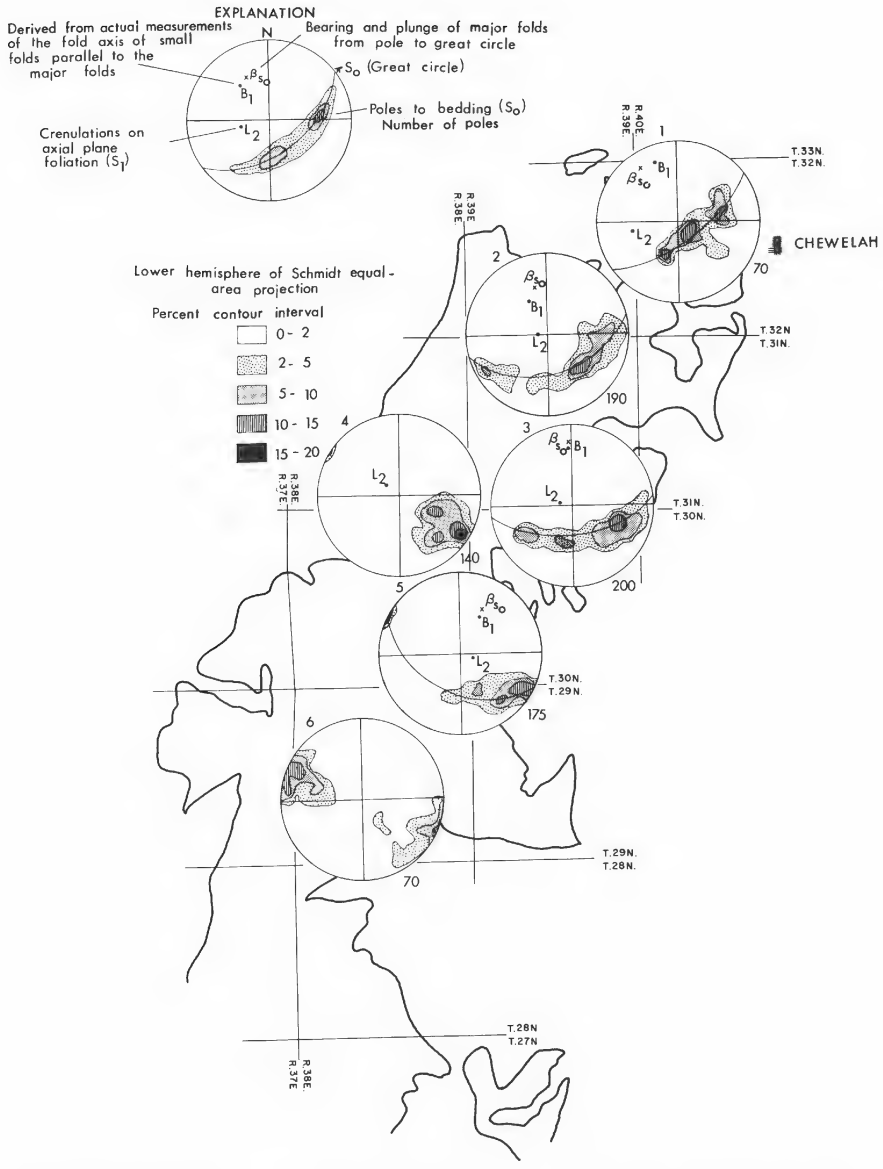


Figure 4. Contoured equal-area projections of poles to bedding and bedding schistosity (S_0).

Joints and Lithology

Joints in the Metasedimentary Rocks

Joint sets in the various metasedimentary units were compared in an attempt to establish their time of formation. An analysis of joint geometry was made for each of the six

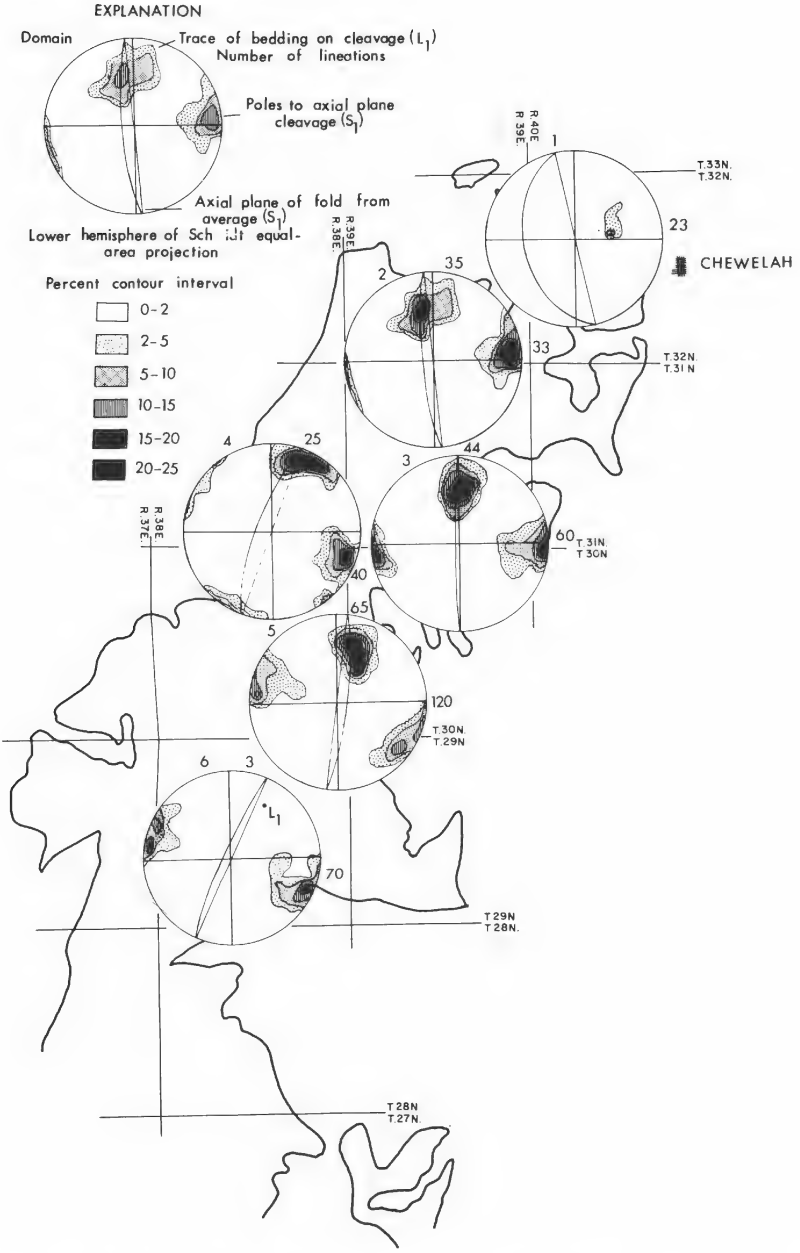


Figure 5. Contoured equal-area projections of poles to axial plane cleavage (S_1) and the trace of bedding on axial plane cleavage (L_1). The trend of the major folds from actual measurements of minor folds is included with (L_1).

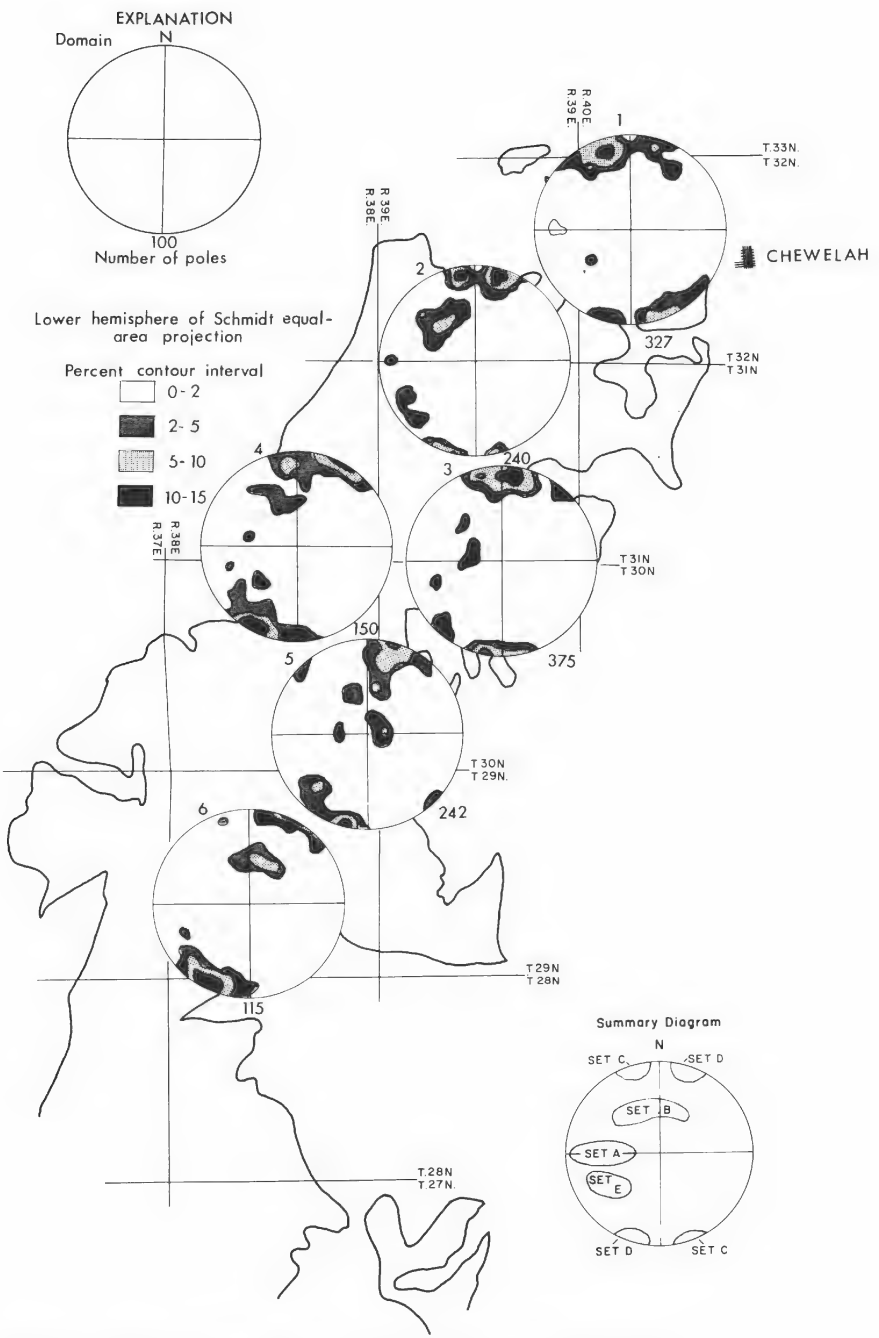


Figure 6. Contour diagrams of poles to joints in the metasedimentary rocks.

domains chosen on the basis of homogeneity of fold trends. Contoured joint-pole diagrams were prepared for each domain (Fig. 6). From these and from the summary diagram (Fig. 6), it can be seen that most joints fall into four or five sets in each domain. These sets and their estimated average attitudes are: set A, due N, variable easterly dip; set B, NE to N to NW strike, variable S dip; set C, N78E, 80 SE; set D, N73W, 88SW; and set E, N20W to N33W, dip 65NE to 75NE. These five sets seem to be present through the entire Deer Trail Group and in the overlying Addy Quartzite. However, all exposures do not necessarily display all five sets.

Data collected adjacent to and west of domain 5, from rocks of the Covada Group of Late Paleozonic and Early Triassic age, suggest the presence of three joint sets (Fig. 7) having approximately the same attitudes as those in the six domains of the report area. The joint sets corresponding to the longitudinal joints and the northeast striking oblique joints appear to be absent. The longitudinal joints are weakly present in the Covada Group, but recordings of these joints do not satisfy the 2 percent contour minimum, therefore they are not shown on Figure 7. The presence of cross joint sets which strike and dip approximately N78E, 81SE; N73W, 88SW and an oblique joint set N20W, 75NE in all metasedimentary formations including the Covada Group suggests that these three sets are post Early Triassic in age.

Joints in the Greenstone Intrusives

All systematic joints already described for the metasedimentary rocks transect the greenstone intrusives as well. At the Red Marble quarry (Secs. 24 and 25, T.31N., R.38E.) a highly schistose, nearly vertical, greenstone dike cuts the Stensgar Dolomite. Quartz, dolomite and magnesite veins lie along the foliation planes within this schistose greenstone. All evidence indicates that the greenstone diking is pre-folding and pre-magnesitization. Measurements of the attitudes of 17 greenstone dikes indicate that they are nearly vertical and have an average strike of N20E (Fig. 8). They trend parallel to the major fold axes and change strike as the folds change trend. These observations suggest that fracturing with a north-northeast trend was active in PreCambrian time and may have been responsible for the preferred direction of diking.

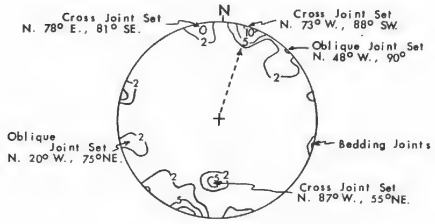
Joints in the Loon Lake Batholith and Associated Plutons

Quartz monzonite and granodiorite compose the larger granitic bodies while aplite, pegmatite, granite porphyry, lamprophyre and andesite occur as dikes, usually with sharp boundaries, within the larger intrusives. A total of 437 readings were taken on joints in the granitic intrusives in areas adjacent to and within granite domains I, II, III, and IV (Fig. 3).

The Cretaceous dikes, stocks and batholith, which are younger than the major folds, contain three joint sets that are present in each of the four granite domains (Fig. 9). The contour maxima to these three major joint sets are plotted on one stereonet (Fig. 10). From the overlapping maxima, average attitudes for these joints were derived for the entire report area; they are N30E, 90; N72W, 84SW; and N33W, 78NE. The joint set which strikes N30E is the only set not present in the metasedimentary rocks.

Near the andesite flows, south of domain 6, porphyritic rhyodacite occurs as dikes within the granodiorite and quartz monzonite. These dikes strike approximately N35E, parallel to one set of major joints in the batholith (N30E, 90) and to other dikes related to the granitic mass. Similarly, aplite and pegmatite dikes not related to the in-

trusive mass also parallel this joint set suggesting that these primary joints were reopened at a later time. No gneissoid texture or flow structures were observed in the granitic rocks, therefore no relation could be established between jointing and granite emplacement. That the major pattern of joints can be correlated between various intrusive bodies suggests that fracturing was the result of regional tectonic forces and is not due to local fracturing induced by magma emplacement.



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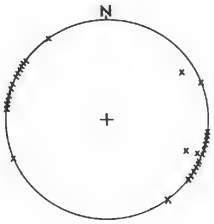

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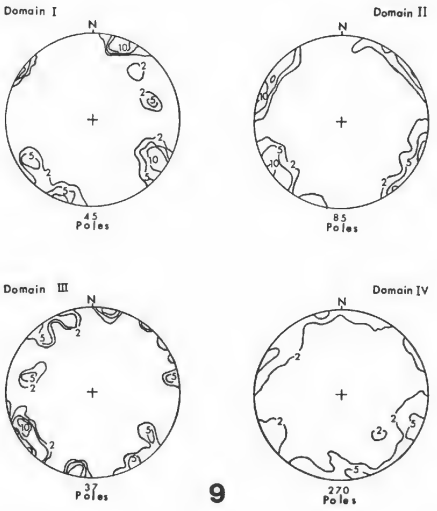

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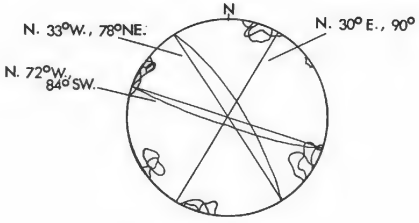

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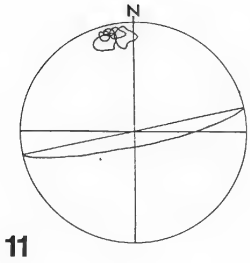
Figures 7-10. Figure 7. Projection of poles to 100 joints in rocks of the Covada Group west of Domain 5. Poles are contoured at 2-5-10 percent intervals. Joint set attitudes are indicated for each contoured maximum of poles to joints. Figure 8. Poles to 17 greenstone dikes showing a preferred orientation in the magnesite belt. Figure 9. Contour diagrams of joints in the granitic masses related to the Loon Lake batholith. Three joint sets are present in all four granite domains (Fig. 3). One set (N33W, 78°NE) is absent from the metasedimentary rocks. Figure 10. Composite of contoured pole maxima to major joint sets present in all granitic bodies of the report area. The overlapping maxima define approximately the attitude of three joint sets.



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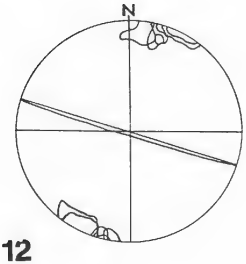

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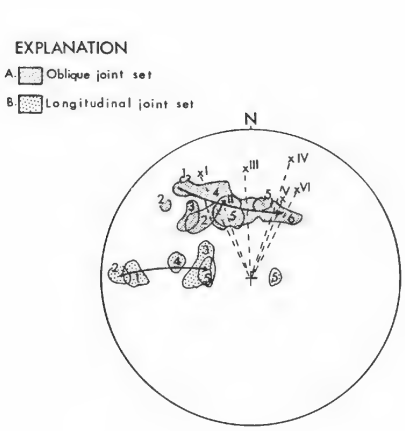

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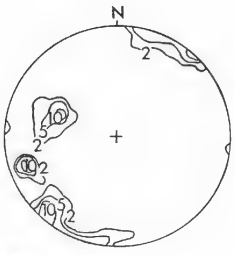

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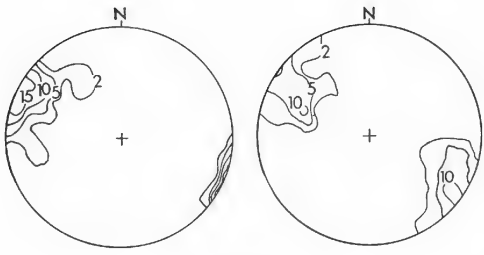

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Figures 11-15. Composite of contoured pole maxima to one set of cross joints. This set is present in the metasedimentary rocks within Domain 1, 2, 3, 4, and 6. The overlapping maxima define the average attitude (N. 78°E., 80°SE.) of this joint set for the entire report area. Figure 12. Composite of contoured pole maxima to the second set of cross joints. This joint set is present in the metasedimentary rocks within all six domains. The overlapping maxima define the average attitude (N. 73°W., 88°SW.) of this joint set for the entire report area. Figure 13. Composite plot of contour maxima of two possible fold-related joint sets in the metasedimentary rocks for each of the six domains. Joint maxima are labelled by number according to the domains they occupy. The bearing and plunge of the major folds in each domain is indicated for each domain identified by Roman numeral. The two arrows indicate a general migration of the joint maxima on the equal-area projection. Figure 14. Contoured equal-area projection of 55 poles to magnesite veins for the entire magnesite belt. Most recordings are from the Red Marble quarry, domain 3. Poles are contoured at 2-5-10 percent intervals. Figure 15. Contoured equal-area projection of poles to mineralized fractures in the metasedimentary rocks (right) and the granitic masses (left).

Joint Pattern in Relation to Folds

In an attempt to determine which joints, if any, may be related to the folding, the geometry of each of the five persistent joint sets in the metasedimentary rock was re-examined (Fig. 6) in relation to the geometry of fold structures, such as fold axes and axial planes. Within the metasedimentary rocks two strong contour maxima are present in the first four domains and in domain 6 (Fig. 6). These maxima were taken from each domain and plotted on two stereograms, Figures 11 and 12. It can be seen from these that the attitude of both joint sets is fairly consistent despite the fact that the folds change trend from domain 1 to domain 6. The contour maxima in Figure 11 overlap to give a small area common to five of the six domains. This "high" defines the average attitude of a joint set striking N78E and dipping 80SE. From domain 1 through domain 4 (Fig. 6) the contour maxima for this joint set decrease in value to domain 5 where it is not present. The contour maxima for the second major set of joints also overlap and define a set which strikes approximately N73W and dips 88SW. This set is present in all six domains and varies little in strike and dip. The above relations suggest that these two major joint sets are not related to the folding but may be younger. A third set is characterized by a rather wide divergence in attitude (N20W to N30W, dip 65NE to 75 NE) that seems not to bear any consistent relation to fold axes. Similarly, a joint set of similar attitude (N33W, 78NE) is well developed in the granitic rocks, which leads us to believe that this third set in the metasedimentary rocks is Cretaceous or younger.

To compare the two remaining joint sets in the metasedimentary rocks to fold geometry, the average bearing and plunge of the folds in each domain was calculated from a combination of the B_1 axis, βS_0, and Li lineations. Both the average bearing of the fold axes and the attitude of the two joint sets from each of the six domains were plotted on one equal-area projection (Fig. 13). On this diagram two arcuate maxima families are indicated by overlapping 2 percent contour maxima defining the attitude of each of the two joint sets in each domain. The arcuate maxima to joints which strike from NE to N to NW display a close geometrical relationship to the folds. This relationship is seen in fold domain 1 where the contour maxima to joints define a plane which is approximately normal to the bearing and plunge of the fold. Although this relationship is not strictly true in fold domains 3 and 4, vectors drawn to indicate the migration of the fold axes from fold domain 1 to fold domain 6 are similar to the vectors drawn to describe the movement of this joint set within the six domains. These relationships are interpreted as indicating that these joints are fold-related extension joints. The second arcuate contour maxima family reflects a set of joints which strike uniformly north but lessen in dip from fold domains 1 and 2 to domain 5. Although these joints are weakly developed in each domain, their significance is emphasized by their presence in five of the six domains. When the attitude of these joints is compared to the average attitude of folds axes and bedding in each fold domain, the joints are found to strike roughly parallel to the fold axes and to dip approximately normal to bedding. This finding suggests that the joints are longitudinal joints related to the folding.

Mineralization Control by Jointing

Magnesite Deposits

All known magnesitized zones are confined to the gray, massive, finely crystalline Stens-

gar Dolomite. Most are conformable with bedding but some are discordant. Study of the magnesite mineralization was centered almost exclusively at the Red Marble quarry (fold domain 3, granite II) since it afforded the best and most accessible exposures. Fifty-five poles to magnesite veins were recorded and are illustrated in Figure 14. Four sets of veins are present, striking and dipping approximately N47W, 85NE; N18W, 75NE; N20E, 45SE; and N75W, 90. A comparison of Figures 9 and 14 shows that of these four magnesite vein sets, the first, second, and fourth correspond rather well to joint sets in three of the four joint domains in granite. The third vein set seems to correspond to a minor joint set present in one granite domain (III). That is, all magnesite-bearing fractures have corresponding joint sets in granite. This finding suggests that magnesitization took place during or subsequent to the emplacement of the granite intrusives.

Metallic Mineral Deposits

Quartz veins carrying scheelite and molybdenite parallel dikes in granite, occasionally transecting aplite and including fragments of aplite. These veins are considered to be genetically related to the Loon Lake batholith. Other quartz veins, presumably younger than the scheelite-molybdenite veins, carry values in lead, zinc, silver, copper, and antimony; they are found in both the metasedimentary rocks and the granitic intrusives. They tend to be lenticular or irregular in shape, pinching and swelling along both strike and dip. Most range from a few centimeters to 6 cms in width.

A stereoplot (Fig. 15) of 92 poles to quartz veins of both kinds, in pregranite and granitic rocks, shows that all mineralized fractures strike from NNE (in granite) to NE (in metasedimentary rocks) and dip from steeply SE, to vertical, to very steeply NW. They are about parallel to pronounced joints in the granite intrusives, many of which are occupied by aplite and pegmatite dikes. The presumption is that steep to vertical northeasterly trending fracturing followed intrusion of the Loon Lake batholith and continued for a long period of time allowing for the introduction of aplite and pegmatite dikes, scheelite-and molybdenite-bearing quartz veins, rhyodacite dikes, and the veins carrying values in lead, zinc, silver, copper, and antimony.

Summary and Conclusion

Attitudes of over 2000 joints in the 500 square km area reveal that most fractures can be categorized as belonging to one of seven distinct joint sets. The identity and the average or range of attitude of each of these is as follows:

Set A: Strike due N; dip E, variable

Set B: Strike NE to N to NW; dip S, variable

Set C: Strike N78E; dip 80SE

Set D: Strike N73W; dip 88SW

Set E: Strike N20W to N33W; dip 65NE to 75NE

Set F: Strike N20E; dip 45SE

Set G: Strike N30E; dip 90

Sets A and B are the oldest joint sets in the magnesite belt. They are absent from the granitic rocks and change attitude in conformity with changes in fold trend in the metasedimentary rocks. Therefore, they are presumed to have been generated during folding

in Jurassic (?) time. Joints of set A are longitudinal; those of set B are transverse and extensional, approximately normal to fold axes.

Joint set C is thought to be younger than sets A and B because it has a remarkably constant orientation throughout the fold belt. This observation together with the recognition of its absence from the granitic rocks is interpreted to mean that joint set C is post-folding and pre-batholith in age.

Joint sets D, E, and F are probably all about the same age and related. Sets D and E are very well developed both in the granitic and metasedimentary rocks. Set F is present in a few places in the granitic rocks but absent from the metasedimentary rocks. All three sets and only these three are parallel to magnesite veins. Sets and veins probably all formed shortly after the emplacement of the batholith (Cretaceous). The formation of magnesite at this time is compatible with the mechanism proposed by Rosenberg and Mills (1966) for the emplacement of magnesite.

Set G is the youngest set of all. Joints of this set are well expressed in the granite batholith and may be occupied by aplite and pegmatite dikes thought to be related to the batholith. Rhyodacite dikes and mineralized quartz veins of the magnesite belt also parallel joint set G. Therefore, the fractures of joint set G are thought to have formed over a protracted period of time beginning shortly after the emplacement of the batholith and its concomitant magnesitization and continuing episodically through periods of multiple diking and vein formation.

This study demonstrates how an analysis of systematic joint patterns may be correlated both in space and time with other structural features, helping to place the events that gave rise to the structural features in their proper sequence. The study also suggests that the tungsten and molybdenum mineralization is related to the Loon Lake batholith but the other metallic mineralization is considerably younger, being localized in space by N30E fracturing and in time by Tertiary volcanic activity.

Acknowledgments

The data on which this paper is based were gathered by the first author in partial fulfillment of the requirements for an M.S. degree in Geology (1970) at Washington State University, Pullman, Washington, under the direction of the second author. Bear Creek Exploration Company generously provided financial assistance by way of a Research Fellowship in support of the field work.

Appendix

Description of Joints

Joints striking within 15 degrees of the fold trend are longitudinal joints. Those striking within 15 degrees of perpendicular to the local structural grain are cross joints. All others are classified as oblique joints. Over 50 percent of the joints in the metasedimentary rocks are cross joints. Approximately 10 percent are longitudinal joints.

Cross Joints

Cross joints are generally smooth, planar fractures present in all lithologies. Those in the Huckleberry Conglomerate are not deflected by the quartzite clasts. Plumose structures are present on cross joints in some medium- to fine-grained rocks. Such joints have good persistence and regularity and an average spacing of 0.3 m between joint surfaces. More than 700 attitudes were recorded for cross joints in the metasedimentary rocks.

Longitudinal Joints

Longitudinal joints are present throughout the magnesite belt. About 140 attitudes were recorded. Approximately 61 percent of these joints dip east, 33 percent dip west, and 6 percent are vertical. Their orientation is related to the geometry of the larger parasitic folds. They are roughly normal to bedding and vary in dip as the bedding changes dip. They are curved, rough, and irregular fractures with moderate to poor persistence, good to moderate regularity, and an average spacing of 0.6 m.

Oblique Joints

Oblique joints are curved, with rough irregular surfaces and an average spacing of 0.6 m. They are moderately persistent in all lithologies and have moderate to poor regularity.

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Association News

The 52nd annual meeting of the Association was held at Western Washington University on March 29, 30, and 31, 1979. There were 163 contributed papers in addition to the symposium "Ecology of Alaskan Arctic Beaches." Dr. John Crow, Professor of Botany at Rutgers University, was the keynote speaker at the banquet. His address, "Wetland Values: Facts vs. Fiction," stressed economic as well as ecologic importance of Alaskan wetlands.

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Constitution revised:

The following revisions to the constitution were adopted by the members at the annual noon business meeting.

Article VI Committees

4. Research Grants Committee. The committee shall consist of three members, each to serve for three years. The President of the Association shall appoint one new member each year. The committee member in his/her third year shall serve as committee chairperson. This committee shall consider requests for grants from the Research Fund and recommend to the Board of Trustees candidates for grants.

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William R. Rayburn
Secretary

Errata:

Program and Abstracts, 52nd Annual Meeting, p. 31, Paper #84. Senior author should be Scott C. Monroe, Department of Geology, Western Washington University.

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The Zooplankton Dynamics of a Eutrophic Reservoir: Long Lake, Washington[3]

Abstract

The effect of cultural eutrophication on the zooplankton community of Long Lake, Washington, was described in terms of composition and standing crop. The major populations were analyzed according to their dynamics and productivity. Various population parameters were related to determine physical, chemical, and biological conditions of the reservoir.

Standing crop estimates for 1972 and 1973 indicated *Daphnia retrocurva* Forbes to be the dominant zooplankter, and it apparently outcompeted all other grazers except *Diaptomus siciloides* Lilljeborg, which assumed dominance in October. Intracyclopoid predation appears to have caused the ultimate displacement of both *Cyclops bicuspidatus thomasi* Forbes and *Cyclops vernalis* Fischer by *Mesocyclops edax* (Forbes). Biomass and secondary productivity were greater in 1973, largely a result of increases in *D. retrocurva* and *D. siciloides*.

The species of zooplankton present may have been regulated by phytoplankton composition, while grazing pressure probably modified the structure of the phytoplankton community.

Introduction

Long Lake, an impoundment of the Spokane River, has been documented as eutrophic on the basis of primary productivity, chlorophyll *a* concentrations, nutrient concentrations, and hypolimnetic oxygen depletion (Soltero *et al.*, 1973; 1974a). The major source of nutrient enrichment influencing the trophic status was effluent from the Spokane, Washington, primary sewage treatment plant.

The major objective of this investigation was to determine the zooplankton dynamics of this eutrophic reservoir. The zooplankton community was described in terms of composition and standing crop. In addition, the major component populations were analyzed according to their population dynamics and productivity. These results were related to the determined physical, chemical, and biological (phytoplankton) conditions of the reservoir.

Description of the Study Area

Long Lake is located approximately 24 km northwest of Spokane, Washington (Fig. 1).

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The reservoir is approximately 35 km long, has a maximum surface area of 208 x 10^5 m^2, and a volume of 305 x 10^6 m^3. A maximum depth of 54.9 m is found at the base of the dam; mean depth is 15 m.

Five permanent sampling stations were established over the former river channel. Station 0 was located just behind the dam, with the remaining four stations located at 8 km intervals up the reservoir.

Methods and Materials

A total of 33 cruises was completed during the study (6 May 1972-17 December 1973). Thirteen cruises were conducted during each of two intensive study periods, 24 June-18 September 1972 (mean sampling interval, 7.2 days) and 19 June-29 September 1973 (mean sampling interval, 8.6 days).

Physical and Chemical Parameters

At each station, temperature, dissolved oxygen, pH, and conductivity were determined *in situ* at 3-m intervals from surface to bottom with a Hydrolab ^{R} Surveyor (model 6). Water samples were also collected at 3-m intervals and analyzed in the laboratory for turbidity, orthophosphate, nitrate nitrogen, nitrite nitrogen, ammonia nitrogen, and total alkalinity in accordance with the American Public Health Association (1971).

Phytoplankton Standing Crop and Primary Productivity

Water samples were collected from the surface to the lower limit of the euphotic zone usually at 2-m intervals. Equal volumes of the euphotic zone samples were combined and the composite was used for phytoplankton enumeration. Cell volumes and counts per unit volume of water were determined for each taxon utilizing the sedimentation method described by Schwoerbel (1970).

The method of Ryther and Yentsch (1957) as modified by Martin (1967) was used to estimate primary productivity.

Zooplankton

Oblique tows were made with a Clarke-Bumpus sampler (20 mesh net and cup) because of irregularities associated with natural distributions of zooplankton (Edmondson and Winberg, 1971). Tows were made from the bottom to surface at all stations and from the power penstock elevation (15 m) to the surface at stations 0, 1, and 2. Collections were preserved in the field with formalin (10 percent of final volume) and later stained by adding 0.5 ml of Lugol's solution and 1.0 ml of a saturated Eosin Y- ethanol solution.

In the laboratory 2 ml subsamples were counted in a modified rotary counting chamber (Ward, 1955). Successive subsamples were counted until either 100 organisms or ten 2 ml aliquots had been examined.

Biomass was estimated for all cladoceran and copepod zooplankters using the length to dry weight relationships of LeSeur (1959), Cummins *et al.* (1969), Hall *et al.* (1970), and Peterka and Knutson (1970). Biomass was estimated for the rotifers using the average dry weight per organism as reported by Hall *et al.* (1970).

Instantaneous birth rates, rates of population change, and instantaneous death rates were estimated for the major crustacean zooplankters (see Table 1) using the egg duration method developed by Deevey (1947) and applied to zooplankton populations by

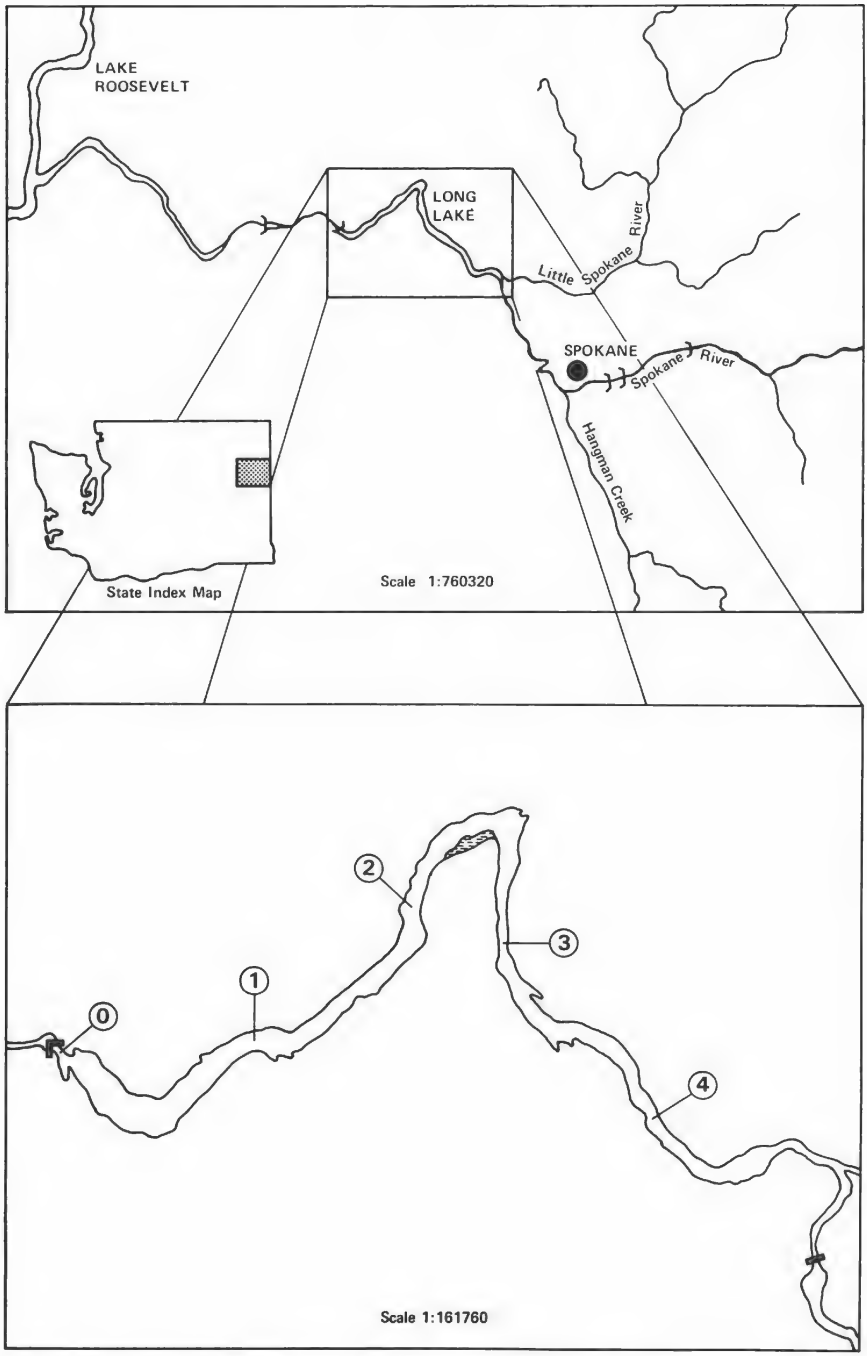

Figure 1. Map of the lower Spokane River system detailing the study area.

Edmondson (1960; 1965), Hall (1964), Wright (1965) and Cummins *et al.* (1969). Specific egg development times were determined using the duration to temperature relationships of Hall (1964), Semenova (1968), Cummins *et al.* (1969), and Malick (1971).

TABLE 1. The major zooplankton species, their abundance (percentage based on #/m²), and dry weight contribution (percentage based on mg/m²) over all stations and dates, Long Lake.

Species	Percent Abundance	Percent Dry Weight Contribution
Rotifera		
Asplanchna priodonta	0.6	0.6
Ascomorpha sp.	7.8	*
Conochilus unicornis	1.4	*
Kellicottia longispina	1.1	*
Keratella cochlearis	28.1	0.1
Lecane luna	4.0	*
Polyarthra vulgaris	4.7	0.1
Trichocerca longiseta	3.5	*
Trichocerca multicrinis	2.3	*
Cyclopoid Copepoda		
Cyclops bicuspidatus thomasi	2.1	1.2
Cyclops vernalis	8.5	5.6
Mesocyclops edax	7.6	8.3
Calanoid Copepoda		
Diaptomus siciloides	11.8	11.9
Grazing Cladocera		
Bosmina longirostris	1.3	0.9
Daphnia retrocurva	10.9	62.9
Diaphanosoma leuchtenbergianum	2.4	6.6
Predaceous Cladocera		
Leptodora kindtii	0.1	1.3

*=less than 0.1%

Secondary productivity was estimated as the sum of individual productivities for the major grazing zooplankters (*Diaptomus siciloides* Lilljeborg, *Daphnia retrocurva* Forbes, *Diaphanosoma leuchtenbergianum* Fischer and *Bosmina longirostris* [Mueller]). Individual grazer productivity was determined using the method of Edmondson (1960; 1968), Wright (1965), and Cummins *et al.* (1969).

Results

Water Quality

During 1973, reduced Spokane River flows resulted in the sewage effluent comprising 2.1 percent of the influent waters to the reservoir; this figure represents approximately a four-fold increase over 1972. The lower river flows of 1973 increased nutrient loading to the reservoir, which promoted excessive algal growth, heightened hypolimnetic anoxia, and increased hypolimnetic concentrations of orthophosphate and ammonia nitrogen over that observed in the previous year (Soltero *et al.*, 1975).

Zooplankton Composition

Thirty-seven species were identified throughout the investigation. Twenty-two species were in the Rotifera, five were in the Copepoda, and ten were in the Cladocera. The rotifer *Keratella cochlearis* (Gosse) was the most abundant species and was identified from

the greatest number of samples, but contributed little dry weight (Table 1). *Daphnia retrocurva*, a cladoceran, was the most prominent zooplankter on a dry weight basis and was third in abundance; the copepod *Diaptomus siciloides* was second on a basis of both dry weight and abundance.

The zooplankton were grouped into five major categories reflecting both taxonomic and trophic differences (Table 1; Fig. 2). Numerically, the Rotifera formed a major group during both study periods; they were less important on a dry weight basis, comprising only 1.1 percent and 0.3 percent of the 1972 and 1973 standing crops, respectively.

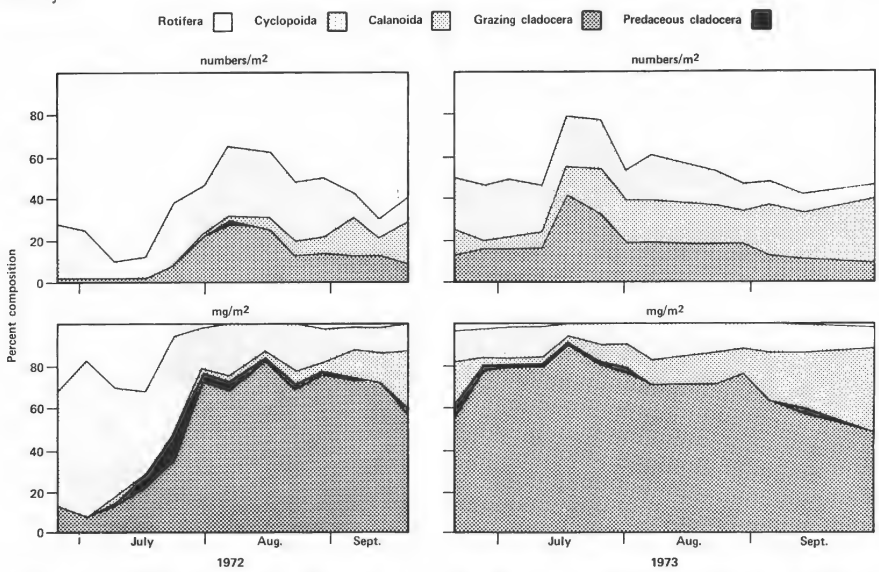

Figure 2. Percent composition (based on #/m² and mg/m²) for selected zooplankton categories during the 1972 and 1973 intensive study periods by sampling date over all stations, Long Lake.

The Cyclopoida made up 18.2 percent and 17.7 percent of the 1972 and 1973 abundance (#/m²), while dry weight standing crop (mg/m²) decreased from 19.2 percent during 1972 to 12.0 percent in 1973. This group was the major contributor to the total biomass in June and early July of 1972, but was not a major contributor in 1973. Calanoida abundance increased from 7.1 percent during 1972 to 16.8 percent in 1973 and from 8.0 percent of the dry weight standing crop in 1972 to 12.4 percent in 1973.

During 1972, the grazing Cladocera attained maximum abundance and biomass in the latter part of July and maintained it through September; in 1973, a maximum was evident from mid-June through September. The predaceous Cladocera were not very abundant and contributed little to the dry weight standing crop during both study periods.

Zooplankton abundance (#/m²) followed biomass estimates (mg/m²) and the correlation coefficient was $r=0.56$ ($P=0.01$) using mean data over all stations for each sampling period.

Zooplankton Seasonal Succession

Successional patterns for the zooplankton were based on mean dry weights over all stations for each sampling date (Fig. 3). During 1972, *Bosmina longirostris* (Mueller) was the major grazing cladoceran in May, June, and the first part of July, while *Diaphanosoma leuchtenbergianum* Fischer followed with a seasonal high in late July to early August. *Daphnia retrocurva* then succeeded *D. leuchtenbergianum* in early August and

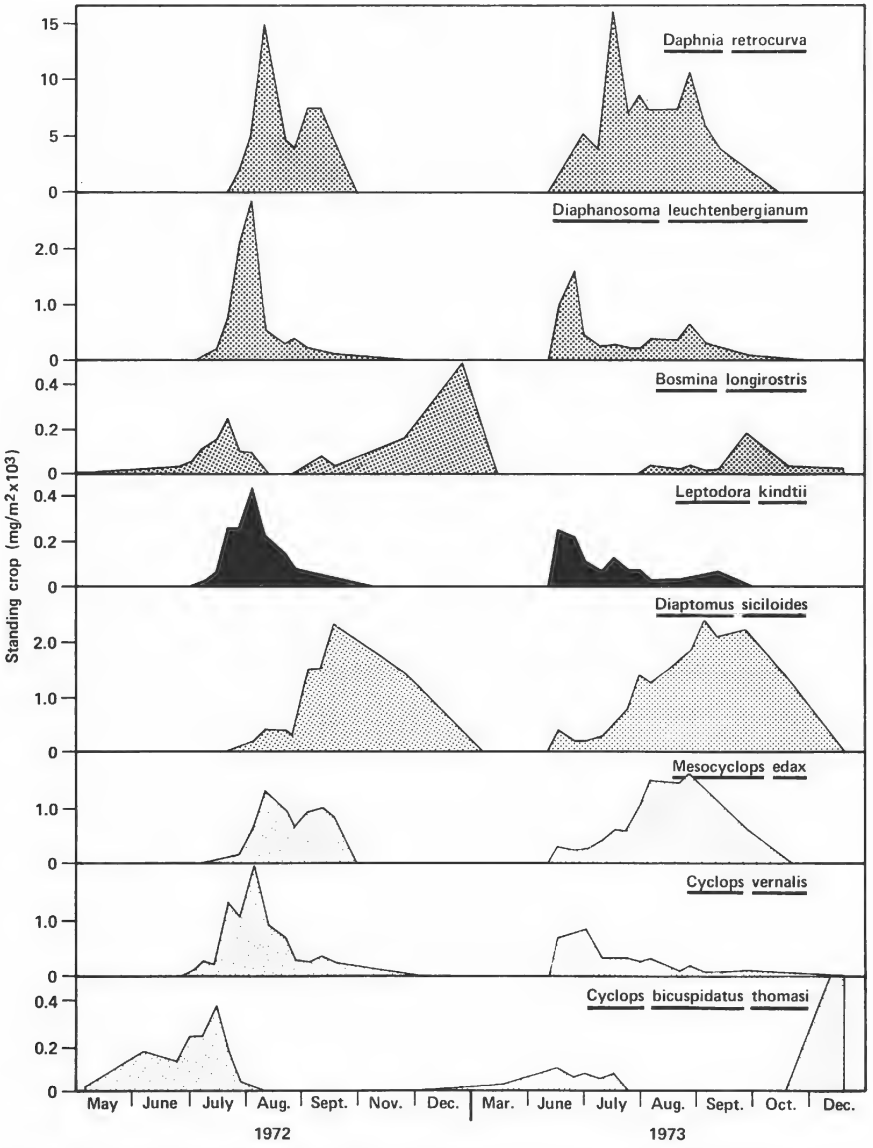

Figure 3. Mean standing crop of the major zooplankters by date over all stations, Long Lake.

maintained dominance through September. *Bosmina longirostris* was again the major contributor to the standing crop of grazing cladocerans in November and December, 1972. In 1973, *D. retrocurva* was the dominant grazing cladoceran from 19 June through September. *Diaphanosoma leuchtenbergianum* biomass was less in 1973 and a large initial standing crop of *B. longirostris* was not evident.

The mean biomass for *Leptodora kindtii* (Focke), the major predaceous cladoceran, decreased from 132 mg/m^2 in 1972 to 84 mg/m^2 in 1973.

Diaptomus siciloides, the only calanoid copepod identified during the investigation, attained a substantially higher mean biomass in 1973 (1174 mg/m^2) than during 1972 (525 mg/m^2). Maximum biomass was attained in September of both years. *Cyclops bicuspidatus thomasi* Forbes, the cyclopoid copepod in May and June 1972, was followed by *Cyclops vernalis* Fischer in early July. *Mesocyclops edax* (Forbes) was dominant from mid-August through September. In 1973, *C. vernalis* was dominant in June. *Mesocyclops edax* then followed *C. vernalis* in early July and maintained a larger mean standing crop during 1973 than during 1972.

Relationships between Zooplankton Population Parameters and Dry Weight Standing Crops

Relationships between the determined population parameters and dry weight standing crops of the major zooplankters were determined by means of simple correlation analysis using mean data over all stations for each sampling date during the intensive sampling periods. The relationship between *D. retrocurva* and *B. longirostris* biomass was negative ($r=-0.45$, $P=0.05$). Significant positive correlations were apparent in comparing *D. retrocurva* and *D. leuchtenbergianum* rates of population change, r ($r=0.63$, $P=0.01$), instantaneous death rates, d ($r=0.56$, $P=0.01$), and biomass ($r=0.58$, $P=0.01$).

Within the Cyclopoida, the instantaneous birth rate (b) of *C. bicuspidatus thomasi* correlated negatively with the biomass of *M. edax* ($r=-0.61$, $P=0.01$) and d of *C. bicuspidatus thomasi* correlated positively with the biomass of *C. vernalis* ($r=0.56$, $P=0.01$). Positive relationships were found between the b of *C. vernalis* and *M. edax* ($r=0.70$, $P=0.01$) and in comparing the d of *C. vernalis* with the biomass of *M. edax* ($r=0.38$, $P=0.05$).

Positive relationships were also revealed in comparing *D. siciloides* and *M. edax* b ($r=0.50$, $P=0.01$) and biomass ($r=0.71$, $P=0.01$). *Diaptomus siciloides* biomass correlated negatively with *M. edax* r ($r=-0.53$, $P=0.01$).

Effect of Limiting Habitat

Mean zooplankton dry weight was determined for the 15 m depth to the surface and bottom to surface tows over stations 0, 1, and 2 for each date during the intensive study periods. The ratios of the 15 m to surface and bottom to surface biomass were then calculated. A ratio near unity would indicate that the lower depths were essentially void of zooplankton. In 1972, the ratio became greater than 0.90 on 22 July and remained there through 11 September. In 1973, the ratio exceeded 0.90 on 19 June and remained there through 4 September. Correlation between the ratio and the mean chemical parameters for each date over stations 0, 1, and 2 during the 1972 and 1973 intensive study periods revealed positive relationships with orthophosphate ($r=0.35$, $P=0.05$) and nitrite nitro-

gen (r=0.38, P=0.05). A strong negative relationship was evident in comparing the ratio with dissolved oxygen concentrations (r=–0.72, P=0.01).

Zooplankton-Phytoplankton Standing Crops and Productivity Relationships

Substantial increases in the grazing Cladocera corresponded with decreases in the Bacillariophyceae, primarily *Fragilaria crotonensis* Kitton, *Melosira italica* (Ehr.) Kutz., *Melosira granulata* (Ehr.) Ralfs.; and the Cryptophyceae, primarily *Cryptomonas* sp. (Fig. 4). The maxima of the grazing Cladocera corresponded with increases in the Chlorophyceae, primarily *Sphaerocystis schroeteri* Chod., during both years.

Mean values for both primary and secondary productivity were determined for each sampling date over all stations (Graham, 1975). The major grazing zooplankters comprised 97.5 percent of the total zooplankton biomass over both years. Peaks in secondary productivity corresponded with decreases in primary productivity except on 14 August 1972, when both attained maximum values.

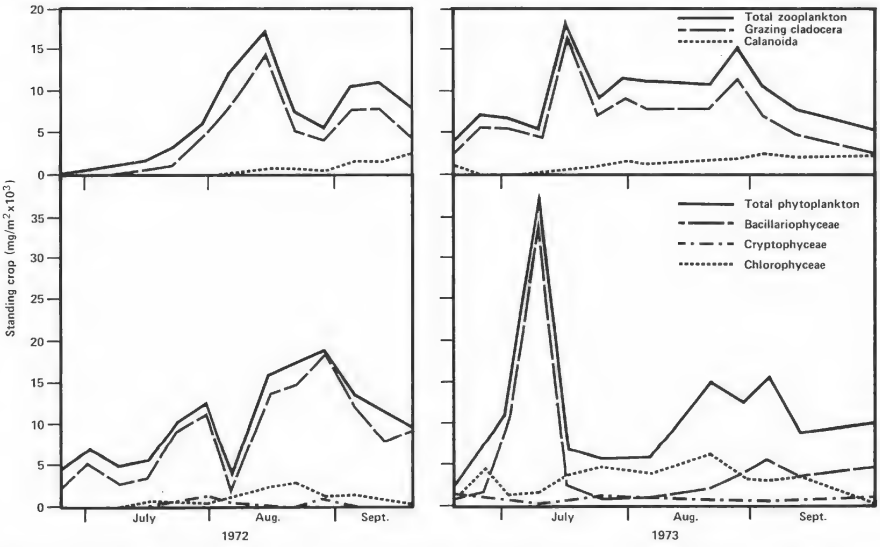

Figure 4. Mean zooplankton and phytoplankton biomass by date over all stations, Long Lake.

Discussion

Mean zooplankton abundance over all stations decreased from 4.71 x 10^6 organisms/m^2 in 1972 to 3.68 x 10^6 organisms/m^2 in 1973, while mean biomass increased from 6.98 g/m^2 in 1972 to 9.70 g/m^2 in 1973. These changes resulted from the Rotifera attaining greater abundance (#/m^2) in 1972 whereas the Calanoida and grazing Cladocera were more numerous and appeared to reduce the Rotifera competitively during the more eutrophic 1973 growing season. Hall *et al.* (1970), in their investigation concerning the dynamics and structure of aquatic communities, determined that the rotifer population was reduced when the larger grazing cladoceran *Ceriodaphnia* was dominant in ponds with high nutrient levels. Brooks (1969) hypothesized that the larger herbivorous zooplankters not only compete more efficiently for the fine particle matter (1-15 mi-

crons), but can also ingest larger particles. Burns (1968) determined that the larger grazing Cladocera can ingest particles up to 70 microns in length.

Similar competitive patterns were observed during this study for the major groups of zooplankters. Within the grazing Cladocera, an increase was observed in the standing crop of *D. retrocurva* in 1973; at the same time, standing crops of *B. longirostris* and *D. leuchtenbergianum* decreased. The significant negative correlation between *D. retrocurva* and *B. longirostris* biomass suggests competitive displacement of the smaller *Bosmina* by *Daphnia. Diaphanosoma leuchtenbergianum* appeared to coexist with *D. retrocurva* based on a comparison of population dynamics, but maintained a reduced standing crop when *Daphnia* was dominant.

Also within the Cyclopoida, *M. edax* maintained the largest standing crop in 1973, whereas *C. vernalis* maintained the largest standing crop throughout most of 1972. Reduced standing crops of both *C. vernalis* and *C. bicuspidatus thomasi* resulted in a small decrease in the cyclopoid biomass in 1973 compared to that of 1972. This finding may reflect both a reduction of preferred prey species (rotifers and small cladocerans) and intercyclopoid predation (Anderson, 1970). Predation on *C. bicuspidatus thomasi* by *C. vernalis* and of *C. vernalis* by *M. edax* was suggested by the significant positive correlations between biomass of the predator and the instantaneous death rate of the prey as suggested by Cummins *et al.* (1969). This hypothesis is consistent with the premise of Anderson (1970) that co-dominance between predaceous copepods of different species is unlikely because each species is a potential predator on the other.

A reduced standing crop of the predaceous Cladoceran, *Leptodora kindtii*, was observed in 1973 and this reduction possibly reflects a decrease in suitable habitat during the growing season. In 1972, mean hypolimnetic dissolved oxygen concentrations were below one mg/l between 14 August and 18 September (Soltero *et al.*, 1974b). Maximum oxygen depletion was observed during the first part of September when the mass of water below the 21 m depth was anaerobic. In 1973, mean hypolimnetic oxygen concentrations were less than one mg/l between 2 July and 29 September (Soltero *et al.*, 1975). The entire hypolimnion (that mass of water below 15 m) was essentially anaerobic from mid-July to mid-September.

Daphnia retrocurva and *D. siciloides* appear to be indicative of excessive nutrient enrichment and resultant hypolimnetic oxygen depletion. Both species are epilimnetic inhabitants, as opposed to those forms that migrate throughout the water column (Tappa, 1965; Arnold, 1969). Consequently, in waters where the hypolimnion is lost as suitable zooplankton habitat, increased abundance of these species may result.

Phytoplankton composition can regulate the structure of the zooplankton; conversely, zooplankton grazing can influence the composition of the phytoplankton. Large standing crops of the Bacillariophyceae, Cryptophyceae and nannoplankton are effectively grazed by the larger, more efficient herbivorous zooplankters (Hilbricht-Ilkowska *et al.*, 1972; Porter, 1973). On the other hand, when phytoplankton standing crop is dominated by Cyanophyceae and Dinophyceae, standing crops of the larger grazing zooplankters are often reduced (Brooks, 1969) and abundance of the smaller zooplankters increases (Hillbricht-Ilkowska *et al.*, 1972). Thus, the increased standing crops of the Bacillariophyceae and Cryptophyceae observed in Long Lake during 1973 may have selected for a zooplankton community that was dominated by the larger herbivorous zooplankters (*D. retrocurva*, *D. siciloides*, and *D. leuchtenbergianum*).

Composition of the phytoplankton may have been altered by grazing pressure. Grazing may have contributed to the decline of Bacillariophyceae and Cryptophyceae

standing crops during both years of study, although nutrient depletion and light limitation may also have been causative factors (Gasperino, 1974). Furthermore, zooplankton maxima were accompanied by significant increases in the chlorophycean standing crop, specifically *Sphaerocystis schroeteri* Chod. This colonial organism is encased in a thick gelatinous sheath which allows it to pass through the digestive tracts of grazing zooplankton and remain viable. Ingestion and excretion apparently fractures colonies, exposing more cells to available nutrients and resulting in increased standing crop (Porter, 1973).

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The Role of Actively Moving Sand Dunes in the Maintenance of an Azonal, Juniper-Dominated Community

Abstract

An edaphically controlled pattern of cyclic community development is described for azonal vegetation dominated by a disjunct population of western juniper (*Juniperus occidentalis* Hook.). The role of actively moving sand dunes in the maintenance of this unique vegetation is discussed. It is speculated that the sand dune-vegetation union had a periglacial origin. Nomenclature follows Hitchcock and Cronquist (1973).

Introduction

Vegetation associated with sand dunes has long been a subject of ecological investigation (Cowles, 1899; Olson, 1958; Morrison and Yarranton, 1973). Such studies typically have dealt with patterns of plant community development following stabilization of the dunes. This paper presents results of a study at an isolated tract of western juniper (*Juniperus occidentalis* Hook.) associated with moving sand dunes in eastern Washington. The juniper-dominated vegetation of this dune complex exists in sharp contrast to the surrounding treeless shrub-steppe vegetation (Daubenmire, 1970). Although western juniper forms extensive savanna-like forests in the southern Cascade Mountains of eastern Oregon (Franklin and Dyrness, 1973), the disjunct population reported here is unique in Washington (Sudworth, 1908).

A pattern of cyclic community development is imposed by movement of the sand dunes. Analysis of this cyclic development, estimates of the rate of dune movement, and the post-glacial history of the area allow speculation on the origins of the dune-vegetation union.

Site Description

The study area (Fig. 1) is located within the Pasco basin of eastern Washington (46° 25'N, 119°W). The sand dune complex lies 26 km northeast of the junction of the Columbia and Snake Rivers, approximately 300 m above sea level. The Pasco basin represents one of the driest areas in the Pacific Northwest, with a mean annual precipitation of 19 cm, over 50 percent of which falls from November to February. Mean temperatures for July and January are 24°C and 0°C, respectively (NOAA, 1977).

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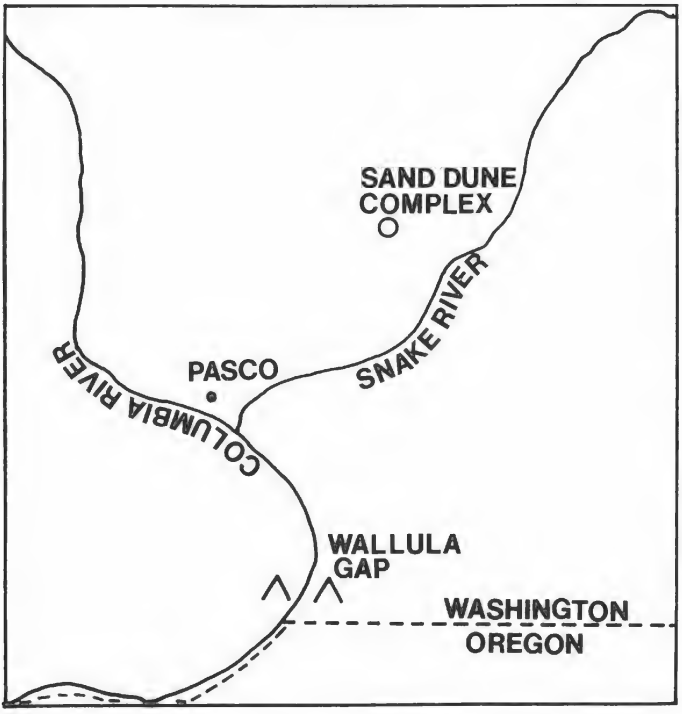

Figure 1. Location of sand dune complex northeast of the junction of the Columbia and Snake Rivers.

The treeless natural vegetation of the Pasco basin is characterized by Daubenmire (1970) as steppe and shrub-steppe and is dominated by grasses and forbs or sagebrush (*Artemisia tridentata* Nutt.). Western juniper is, with the exception of the sand dune population, restricted to a few isolated individuals along the Columbia and Snake Rivers (Sudworth, 1908).

The complex of sand dunes and its associated vegetation cover an area of approximately 1000 ha. The sand dunes may reach a height of 40 m. The direction of the prevailing wind, and therefore of dune movement, is toward the northeast.

Methods

Vegetation development behind two moving sand dunes was studied. The dunes, located in the southern part of the dune complex (N½, Sec. 32, T11N, R32E), were chosen for the apparent representativeness of their associated vegetation. Quantification of vegetation development behind the moving sand dunes was accomplished with a line intercept technique (Reiners *et al.*, 1971). For each dune, 10-meter-long transects were established perpendicular to a baseline running from the center of the dune crest to the base of the dune immediately to windward (in this portion of the dune complex, distances between dunes average about 400 or 500 m). The perpendicular transects were established at 10- to 20-m intervals along the baseline. The shorter sampling interval was

used near the dune crest where the rate of change in community development is greatest.

The percentage of canopy cover of each plant species occurring at a given distance behind the dune crest was estimated from the total amount of each species' canopy transected by the 10-meter-long line at that sampling point (Buell and Cantlon, 1950). The sampling included mosses as well as vascular plants. The age of each tree on the area behind the two dunes was estimated from ring counts. Increment cores were taken from as near ground level as possible.

Results

There is a distinct and consistent pattern of vegetation behind each of the observed sand dunes (Fig. 2). Casual observation suggests progressive zones of development. Immediately to the windward side of each dune crest is a blowout zone extending approximately 200 m behind the crest of the dune. Vegetation in the dune tract ranges in development from a single species of grass in the area adjacent to the blowout zone to a relatively complex assemblage of species dominated by juniper and large shrubs more distant from the dune crest.

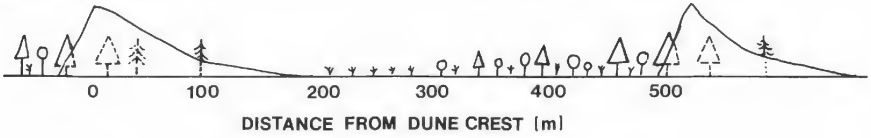

Figure 2. Generalized representation of dune-generated pattern of community development.

Table 1 represents the percentage of cover of individual plant taxa present at increasing distances behind the crest of a single dune. While there are minor differences in cover for individual species within the two tracts sampled, the patterns of community development are quite similar.

Certain species demonstrate different patterns of development relative to distance behind the dune crest. *Rumex venosus* Pursh., a strongly rhizomatous species, is limited to the slipface on the leeward side of the dunes. *Elymus flavescens* Scribn. and Smith, a rhizomatous grass, is restricted to the most disturbed sites on the windward side of the dunes. *Agropyron dasystachyum* (Hook.) Scribn., in contrast, reaches its highest cover in the area immediately behind the blowout zone (Fig. 3). With increasing distance behind the dune crest, its cover is sharply decreased. A small amount of *A. dasystachyum* (Hook.) Scribn. was observed in the vicinity of a small blowout at approximately 410-430 m from the dune crest. Cover increases sharply at the end of the tract as sand from another dune advances.

Other grasses reach their maximum importance in an area of the dune tracts well beyond that dominated by *A. dasystachyum* (Hook.) Scribn. In the case of the first dune tract, *Festuca idahoensis* Elmer reaches its maximum cover approximately 100 m farther from the dune crest than does *A. dasystachyum* (Hook.) Scribn.

The shrubs, of which *Purshia tridentata* (Pursh.) DC and *Chrysothamnus* spp. Nutt. are the most important, have a slightly different pattern of development (Fig. 3). They are first encountered nearly 300 m behind the dune crest. Cover increases to 25 or 35 percent, but decreases in the vicinity of sand disturbance (e.g., the small blowout area and at the end of the tract). The juniper increase in density, average size, and age with

TABLE 1. Percentage of cover as a function of distance from a dune crest (with the exceptions noted in the text, the first 200 m are bare).

Species	Distance from Dune Crest (m)																				
	200	210	220	230	240	250	260	270	280	290	300	310	320	340	360	380	400	420	440	460	480	500
Shrubs																						
Atriplex spinosa (Hook.) Collotzi									2	1		tr		tr			3					
Chrysothamnus nauseosus (Poll.) Britt.				4	tr	4	2	9	2	1	10		tr	7	9			5		2		6
Chrysothamnus viscidiflorus (Hook.) Nutt.								2	11	tr	6			1	5				2		12	
Purshia tridentata (Pursh.) DC.										7	21	30	26	18	24	36	3	12		34	25	13
Forbs																						
Achillea millefolium **L.**					1	tr	tr	2	2	tr	2	tr	1	tr	1	1	tr	1	2	1	2	2
Balsamorhiza sp. Nutt.									tr									tr				
Castilleja sp. Mutis ex L.F.																	tr					
Cerastium nutans Raf.			6	5	3	2	4	3	12	5	6	10	14	9	10	6	2	1	2	1		
Crocidium multicaule Hook.											tr											
Descurainia sp. Webb. & Berth			tr			tr	tr	tr		tr	1	tr	1	9	1	2	tr	1	1	2	1	tr

TABLE 1 (Cont'd)

Erysimum occidentale (Wats.) Robins									tr													
Fritillaria pudica (Pursh.) Sprang														tr			tr			1		
Lomatium sp. Raf.																			tr	2		
Microsteris gracilis (Hook.) Greene			tr	1	3	4	2	2	2	1	1	2	1	2	2	tr	1	1	tr			
Phlox sp. L.																	tr	11	12	10	5	
Rumex venosus Pursh.																					tr	
Mosses			tr	4	3	6		7	6	4	1	10	1	8	tr	3	2					
Grasses																						
Agropyron dasytachyum (Hook.) Scribn.		10	11	7	2	1	1	1	1		1	tr			tr		2		tr	1	8	
Bromus tectorum L.		tr	1	2	4	8	10	5	3	2	3	2	6	12	4	tr	4	1	2	6		
Elymus flavescens Scribn. & Smith	1	4																				
Festuca idahoensis Elmer[1]										6	7	18	34	tr	13	4	1	1	tr			
Oryzopsis sp. Michx.						1																
Poa spp. L.				tr	tr		1	3	6	8	3	5	7	2	31	2	1	1	2	2		

[1]These data were collected in March and the authors admit to some uncertainty in the identification of this taxon beyond its genus.

increasing distance behind the dune crests. Figure 4 represents the relationship between age and distance behind the dune crests for individual trees within the two sampled dune tracts.

Discussion

There are two basic assumptions implicit in the following discussion of the vegetation-sand dune union. The first is that the rate of sand dune movement has, in general, remained relatively constant. The second is that distance behind a dune crest is directly

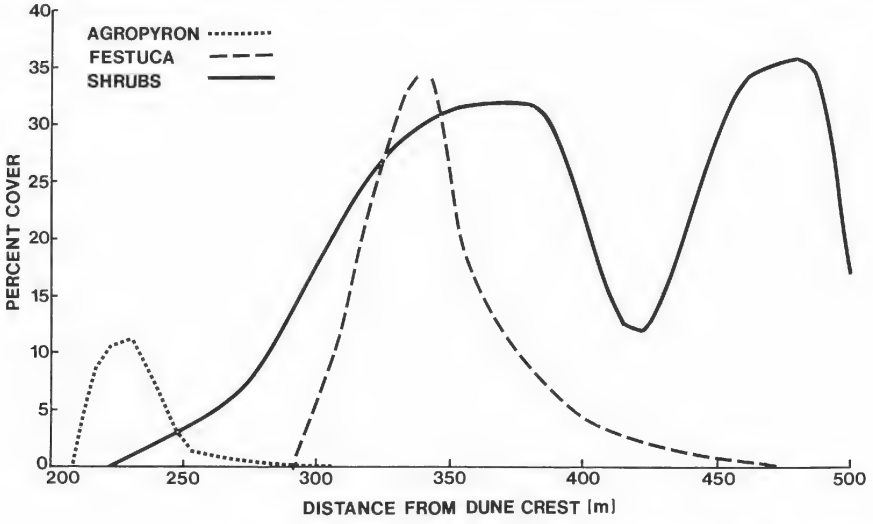

Figure 3. Percent cover as a function of distance behind dune crest for shrubs and two grasses (functions are polynomial expansions of smoothed data).

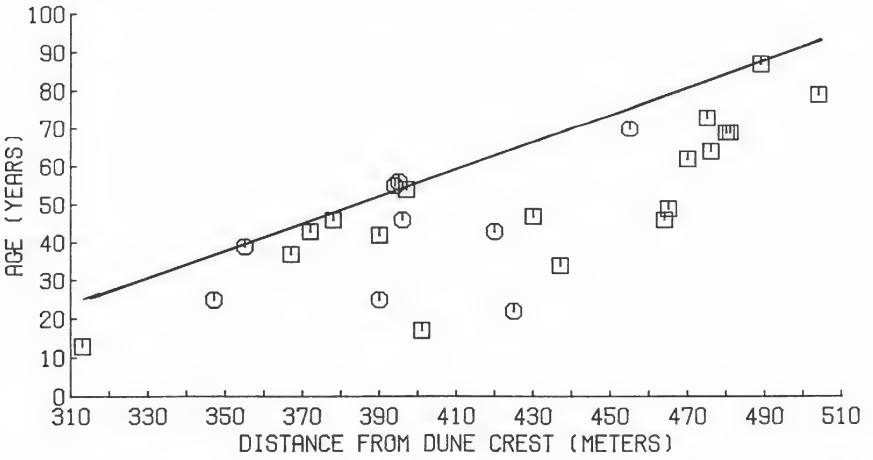

Figure 4. Estimates of age and distance from dune crest for individual juniper of two dune tracts (indicated by circles and squares).

related to the length of time that location has been available for colonization by plants. Similar assumptions are commonly made in the application of the chronosequence approach to the study of community and edaphic development (Stevens and Walker, 1970). Although this approach is not completely satisfactory, it is a commonly employed alternative to long-term monitoring of permanent plots.

A sand dune moves in the direction of the prevailing winds. Its rate of movement is a function of many factors including wind speed, grain size, and the height and shape of the dune. Movement of the dune results when sand is plucked by the wind from behind the dune crest and blown up and over the crest. Thus, the depth of sand at a fixed point in front of the dune crest is gradually increased; at the same time, the depth of sand at a fixed point behind the crest is gradually lowered. This lowering and leveling of the sand surface, combined with the fact that the dune crest and its associated high-speed winds are moving farther away, results in the removal of a decreasing amount of sand.

The lowering of the sand surface eventually slows to the extent that colonization by some plant species is made possible (e.g., *A. dasystachyum* [Hook.] Scribn.). The presence of these plants presumably enhances the process of sand stabilization, allowing the establishment of additional species (Morrison and Yarranton, 1973).

The pattern of vegetation development suggested by the data (Table 1) is one of rapid initial establishment and subsequent growth of populations following sand stabilization. Most species present in the dune tracts are found within 50-60 m of the windward side of the blowout zone. The appearance of zones of vegetation in the dune tracts is the result of different rates of establishment for various species combined with increased size of some of the slow growing, long lived species (Drury and Nesbet, 1973).

This process of vegetation development within an individual dune tract is ultimately arrested by the advancement of another sand dune. The sand of the advancing dune overrides and causes death of even the relatively large western juniper as evidenced by juniper snags in many blowout zones. The pattern of sand stabilization and vegetation development is subsequently repeated behind the crest of this second dune. This cyclic pattern of community development is analogous to the wavelike structural pattern described by Sprugel (1976) for certain montane *Abies* forests.

Vegetation of the 1000-ha sand dune complex then consists of a mosaic of plant communities, each appearing in the wake of an advancing sand dune. Individual plants do not move along with the advancing dunes; however, populations and the communities that they compose do move in just this way. The most conspicuous example of such a population is the western juniper. At a particular point on a given dune tract, individual juniper become established, are eventually killed when overridden by a subsequent dune, and are replaced by another population of juniper.

The Pasco basin sand dune complex can be thought of as a mobile habitat, carrying an azonal vegetation across the landscape. Many of the plant species associated with this migrating complex are absent from the surrounding shrub-steppe or grassland vegetation (Daubenmire, 1970). Some species, such as *Agropyron dasystachyum* (Hook.) Scribn., are adapted to the highly disturbed areas immediately behind the blowout zones (Daubenmire, 1970). The limited number of species capable of surviving under such conditions results in reduced interspecific competition. For other species, such as the juniper, the sand apparently provides a critical combination of environmental factors available in but a few habitats outside the sand dune complex.

The virtual restriction within the Pasco basin of western juniper to the sandy soils associated with the sand dunes is probably a function of the more favorable soil moisture regime afforded by these soils in contrast with the finer-textured zonal soils. The occasional juniper occurring in sandy soils along the Columbia and Snake Rivers is apparently exploiting a similar habitat.

A similar situation is described by Berry (1963) for a disjunct stand of ponderosa pine (*Pinus ponderosa* Dougl.) in Oregon. The pine occur on sand deposits and stabilized dunes in an area surrounded by finer-textured soils dominated by species adapted to more xeric conditions. After an examination of soil moisture, Berry concluded that, in this arid environment, sandy soils actually held more available moisture than surrounding fine-textured soils. Chadwick and Dalke (1965) also demonstrated, on the basis of water potential measurements, that greater water availability in sandy soils under arid conditions may be a key factor in explaining the occurrence of *Prunus virginiana* var. *demissa* (Nutt.) Torr. in sand dune tracts in northern Idaho.

The occurrence of a disjunct population of trees is often explained on the basis of some prior change in climate. The population in question is then assumed to be a relic of a previously existing, more widespread population (Oosting, 1956). For example, Moir *et al.* (1973) provide evidence for the relic status of a disjunct stand of ponderosa pine in eastern Oregon. The arguments presented include indications from the pollen record of the previously widespread occurrence of ponderosa pine in the region of sagebrush steppe within which the now isolated stand occurs.

Relic status therefore represents a possible explanation for the existence of the western juniper-dominated vegetation associated with the sand dune complex in the Pasco basin. There is, however, no indication in the pollen record of eastern Washington that western juniper was ever more widespread than it is at present (Hansen, 1947; Mack and Bryant, 1974). In addition, paleoclimatic reconstruction for the region suggests a period of post-glacial climate even more inappropriate for trees than exists at present (Antevs, 1948).

An alternative explanation of the origins of the dune-vegetation union may be found in the origins of the dune complex itself. It seems likely that the sand dunes originated in the exposed bed of glacial Lake Lewis which formed temporarily near the junction of the Columbia and Snake Rivers. Lake Lewis is the name applied to a large temporary lake that formed behind a hydraulic dam at Wallula Gap (Fig. 1) during the Spokane Floods (Daugherty, 1956; McKee, 1972). The failure of a glacial ice dam and the subsequent rapid emptying of glacial Lake Missoula in Montana (Bretz, 1959) resulted in the spectacular discharge of water that eventually flowed through the relatively constricted gorge at Wallula Gap. The backing up of water at this point resulted in the deposition of deep beds of a coarse sand (Flint, 1938). This sequence of geologic events occurred several times during the last glacial episode (Fryxell, 1962).

It is suggested that the origin of the sand dune complex, and the sand dune-vegetation union, may correspond to the last filling and emptying of Lake Lewis. Fryxell (1962) suggests that the last few floods occurred in the period 15,000-20,000 BP. Recent investigations, however, suggest that the last flood may have occurred approximately 12,000 BP (Brown, 1976).

There are several lines of evidence for the speculation that the sand dune complex originated in the exposed bed of Lake Lewis some 12,000 years ago. One such piece of

evidence is the present location of the sand dune complex northeast of the junction of the Columbia and Snake Rivers. This is the expected position of the dune complex assuming a constant direction of migration. This assumption is supported by Lewis' (1960) conclusion that the regional prevailing winds have remained in a northeasterly direction throughout the Pleistocene.

A second approach is to compare a calculated rate of dune migration with an estimate of the current rate of dune advancement. The slope of the line superimposed upon the age-distance data (Fig. 4) represents an estimate of the rate of juniper colonization in the wake of the moving dunes (Leak and Graber, 1974). The indicated rate of advancement is approximately 2.8 m/yr. If the assumption is made that the juniper advancement is ultimately dependent on dune movement, then the rate of juniper advancement becomes an indirect estimate of the rate of dune advancement (Steward *et al.*, 1940). This estimate compares reasonably well with the 3 m/yr rate of dune movement estimated from aerial photographs for a similar dune complex in northern Idaho (Chadwick and Dalke, 1965). The present distance of the dune complex is approximately 26 km from the suggested place of origin near the Columbia River. Assuming a constant rate of dune migration, the 12,000-year estimate for the initiation of dune migration results in a calculated rate of dune movement of approximately 2.2 m/yr. This figure agrees fairly well with the estimate of 2.8 m/yr for the current rate of dune movement based on tree ages.

Conclusion

There are in the literature a number of examples of cyclic, autogenic succession (e.g., Watt, 1947; Stone and Thorp, 1971) and communities whose development is under the influence of wind (Shacklette *et al.*, 1969; Sprugel, 1976). The sand dune vegetation described here, however, differs in that the mobility of the habitat is responsible for the apparent movement of the plant community.

The origin of sand dunes in periglacial deposits has apparently been widespread. In most cases, however, changes in climate or limited amounts of sand have resulted in the rapid stabilization of the dunes by vegetation (Seppala, 1976). The hypothesized origin of the Pasco basin sand dune complex may thus be the result of fairly unusual edaphic and climatic circumstances, specifically large, localized sand deposits resulting from the formation of glacial Lake Lewis and a more or less continuously dry climate.

We suggest that these circumstances resulted in a specific set of edaphic conditions suitable for the establishment of western juniper. This species is otherwise restricted in the area to isolated locations along the major rivers. The sand dune complex may be characterized as an advancing, mobile habitat which is "carrying" its unique vegetation across the landscape. It is an environment that would, in the absence of the sand dunes, be unsuitable for some of the species, the most notable example of which is western juniper.

Acknowledgments

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Integrated Ecology of the Great Basin. Part III: A Preliminary Analysis of Newark Summit, Eureka County, Nevada

Abstract

The Great Basin is a large area containing a wide variety of ecosystems ranging from arid flatlands to alpine peaks. The area contains many possible future resources. Ecology of the land must be documented and understood before human pressures irrevocably change environmental composition. The third article in a five-year period, this article reports on plant and animal communities and their interrelationships. Various abiotic factors are also noted.

Introduction

Named by Fremont in 1845, the Great Basin region of western North America is one of the largest sparsely populated areas in the continental United States. This area contains a wealth of resources ranging from gold and silver of the Comstock bonanza to the more recently discovered oil fields. Consequently, much of the Great Basin is responding to pressures of development that will change the form and structure of the biotic community.

Considered by many to be merely desert, the Great Basin is one of the least scientifically investigated areas remaining in this country, although parts of it have been examined thoroughly with respect to particular plant or animal species. Also, some general surveys of flora or fauna have been made, including Tidestrom (1925), Linsdale (1936, 1938), Hall (1946), Billings (1949), La Rivers (1962), Beatley (1975), and others. Many areas remain undescribed since the early explorers' accounts. We believe documentation of current conditions in the Great Basin is important, both from the point of view of biological history and for help in assessing effects of any further development. Consequently, we have undertaken a multi-year extensive ecological survey of the Great Basin. Each element of this survey is an intensive consideration of the flora and fauna of a particular area and their interactions. This paper semiqualitatively reports our third study site, Newark Summit, Eureka County, Nevada.

Some 508,000 km^2 in area, the Great Basin consists of most of the state of Nevada and parts of Oregon, Utah, California, Wyoming, and Idaho (Billings, 1951). Climate varies with elevation and ranges from arid to semiarid: much of the Great Basin lies east of the rain shadow cast by the Sierra Nevada Moutains. Alpine environment of some high interior peaks contrasts with alkali flats which mark dry lake beds. Basin-range topography is the major physiographic characteristic of the Great Basin. Approximately 90 small basins are separated by mountain ranges with elevations between 1829 m and 4342

m generally lying in a north-south direction (Blackwelder, 1948). Newark Summit, an area of extensive silver mining activity since the 1860s, is located on one such range, the Diamond Mountains. Newark Summit is approximately 9.7 km north of Eureka, Nevada, 39°28′N; 115°50′W, elevation 2286 m. Weather data for a 30-year period prior to 1970 tabulated from the two closest stations show average precipitation for Austin (112.7 km west, elevation 1994 m) of 31 cm and seasonal mean temperatures from 38.9 to -26°C; and for Ely (145 km east, elevation 1906 m) 22.1 cm precipitation with a seasonal average temperature ranging from 37.2 to -32.°C (National Weather Service, 1973).

The Diamond Mountains around the study site increase in elevation another 762 to 914 m and consist primarily of middle to late Paleozoic-Mesozoic marine deposits which include sandstone, silt-stone, conglomerates, limestone, dolomites, and a variety of shales interspersed with volcanic strata. Vegetation in the area is mixed shrub with an association of some Upper Sonoran life zone mammals but chiefly mammals representative of the Transition and Canadian life zones (Hall, 1946).

The Newark Summit area does not represent climax vegetation because the area has been heavily grazed by both cattle and sheep. Range pressure is further increased by feral horses and wild herbivores which share this habitat. As a result, the area was closed to grazing by the Bureau of Land Management. We believe documentation of current plant/animal interactions of Newark Summit is important as a basis for studying effects of overgrazing on small mammal populations.

Methods

General

This study area was visited by the principal investigators and ten research assistants for eight days during July 1976. Various physical characteristics of the site were measured using conventional equipment. Small mammals were identified and their populations estimated using the trap-mark-recapture technique. Invertebrates were sampled. Data to compute standard ecological indicators for vegetation were collected using a combination of line intercept and plot methods.

Plants

The technique follows Odum (1971) and Cain and de Oliveira Castro (1971). From a randomly selected starting point, 1000 m of line intercept was run: line 1, 300 m due west; line 2 formed a perpendicular with the intersection at the mid point 300 m due south; line 3 started approximately 100 m east of the first starting point and was 200 m long, S25E; line 4 was 200 m long N20E from the end point of line 3. Cover provided by each species of shrub was recorded; forb and grass cover was measured by vegetation type only. Slope and exposure of the transects were taken. At systematic intervals of 200 m, five 10 m x 10 m plots were established with one side of the plot coinciding with the line. Along this side, forb and grass cover was estimated in five 1 m^2 subplots with spacing of 1 m between subplots. Using a 1 m^2 frame, complete cover estimate and count by species was made for shrubs within each plot. Incremental soil temperature, pH, and soil moisture data were collected from the surface to 45 cm in each plot. To study floristic presence, plants on the study site were collected and specimens were preserved for identification. Taxonomic references are in accordance with Munz (1970).

Animals

Small mammals were collected using twelve 8 cm x 8 cm x 25 cm live traps set in two of the 100 m^2 plant plots each night. Additional traps were set along the line intercepts and around the study area with all captured animals marked and released. Cans were buried in substrate with the opening level with the surface to collect insects and soil animals. Large mammals, reptiles, and birds were observed, counted, and recorded. Standard mammalian measurements as set forth in Hall (1946) and Ingles (1967) were used; other vertebrates were identified using as reference Stebbins (1966) and Peterson (1969).

Results

A list of plants in the study site as well as abbreviations used in the text for woody species is presented in Appendix A.

Figure 1 shows the percentage of vegetational coverage by plot for each woody species present and for forbs and grasses. ARTR has the highest average percent cover (23.44). Co-dominant shrubs from average percent coverage for 5 plots rank SYVA second (8.22) and PUTR third (6.73). Average percent for forb/grass coverage is 21.4. For plot 1, SYVA has the highest percentage of coverage (20.65); plots 2, 3, and 4 shows ARTR as having the largest percent coverage (29.80, 33.70, and 30.55, respectively); PUTR has the largest percent cover (14.0) in plot 5. Average percent of coverage considering both woody and non-woody species is 63.3 for the five plots.

Percent of vegetational coverage for 1000 m of line intercept is shown in Table 1 by line segment. Again, ARTR has the highest total percent of coverage (19.6), PUTR ranks second (8.5), and SYVA third (7.3). Forb/grass coverage totals 11.7 percent. Total coverage, both woody and non-woody species, for 1000 m of line intercept is 58.3 percent.

Slope and exposure measurements for the four transect segments produced the following data: line 1: slope 5-11° (rolling topography) with an east and west exposure; line 2: slope 12°, exposure south; line 3: no slope, no exposure; line 4: 3° south. Soil pH for all areas tested ranged between 6.23 and 7.1. Normal soil moisture was difficult to measure since between .6 and 1.2 cm of precipitation fell per day during the study period.

TABLE 1. Line intercept data in segments. Percentage of coverage by shrub and tree species and forb/grass. Newark Summit.

	Segment (as a percent)					
	1 (300 m)	2 (300 m)	3 (200 m)	4 (200 m)	Total* coverage	Relative coverage
Species						
ARTR	19.3	29.6	16.8	7.9	19.6	33.6
PUTR	11.0	10.9	2.9	6.4	8.5	14.6
SYVA	11.1	10.1	3.6	1.7	7.3	12.5
CHsp	3.0	3.8	7.0	5.2	4.5	7.7
CHNA	.3		9.8	7.2	3.5	6.0
AMPA	.4				.1	.2
CELE	.3				.1	.2
BERE			.6	14.2	3.0	5.1
forb/grass	17.0	11.2	8.4	7.8	11.7	20.1
	62.4	65.6	49.1	50.4	58.3*	100.0

*adjusted for variances in line length.

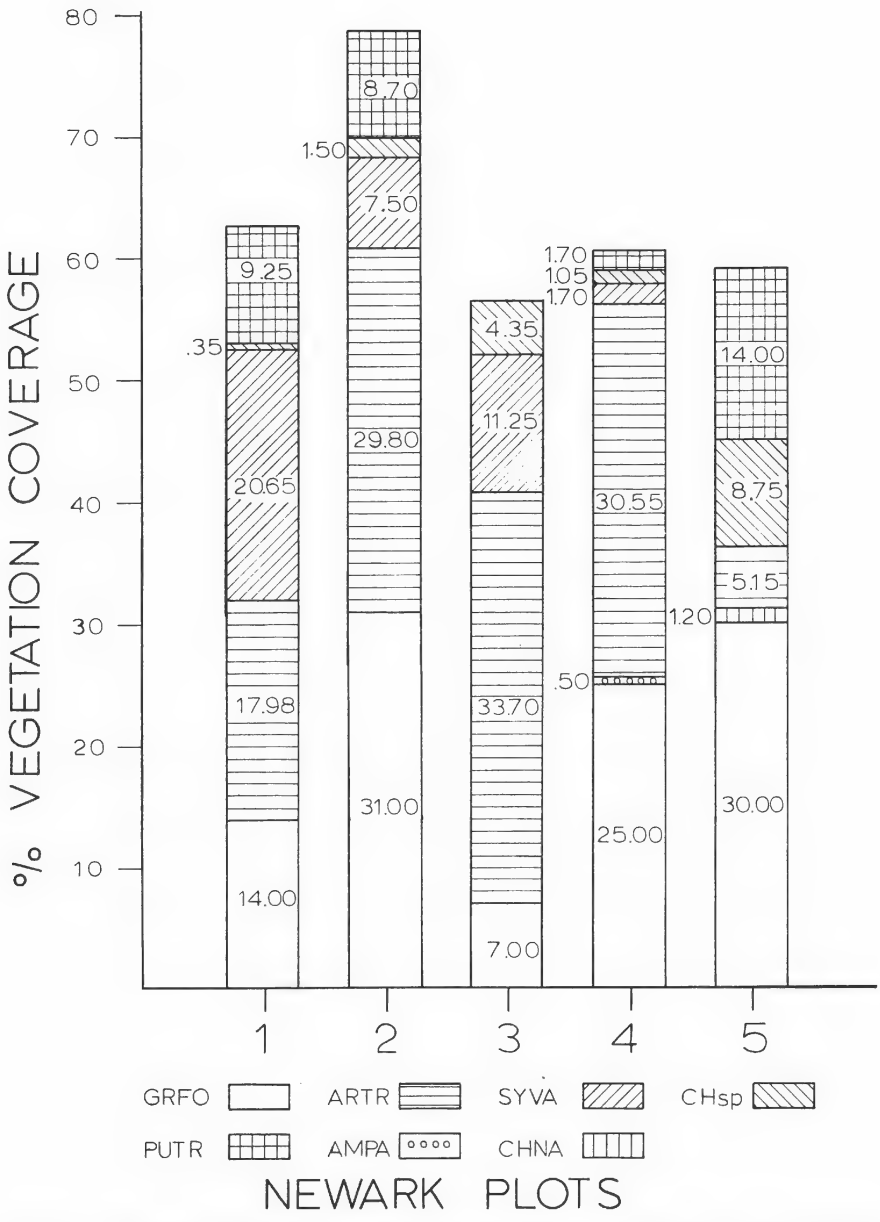

Figure 1. Percentage of vegetational coverage by woody species and forb/grass, by plot. Newark Summit.

Figure 2 shows the number of mammals trapped by species and sex. *Peromyscus maniculatus* was the most frequently captured; 43 males, 27 females, and 20 juveniles, totaling 90 for plots and line segments. *Perognathus parvus* totaled 15: eight males, five females, and two juveniles. Four *Eutamias minimus* and one *Neotoma cinerea* were also captured, all males. Appendix B is a listing of vertebrate species present and observed in the study site.

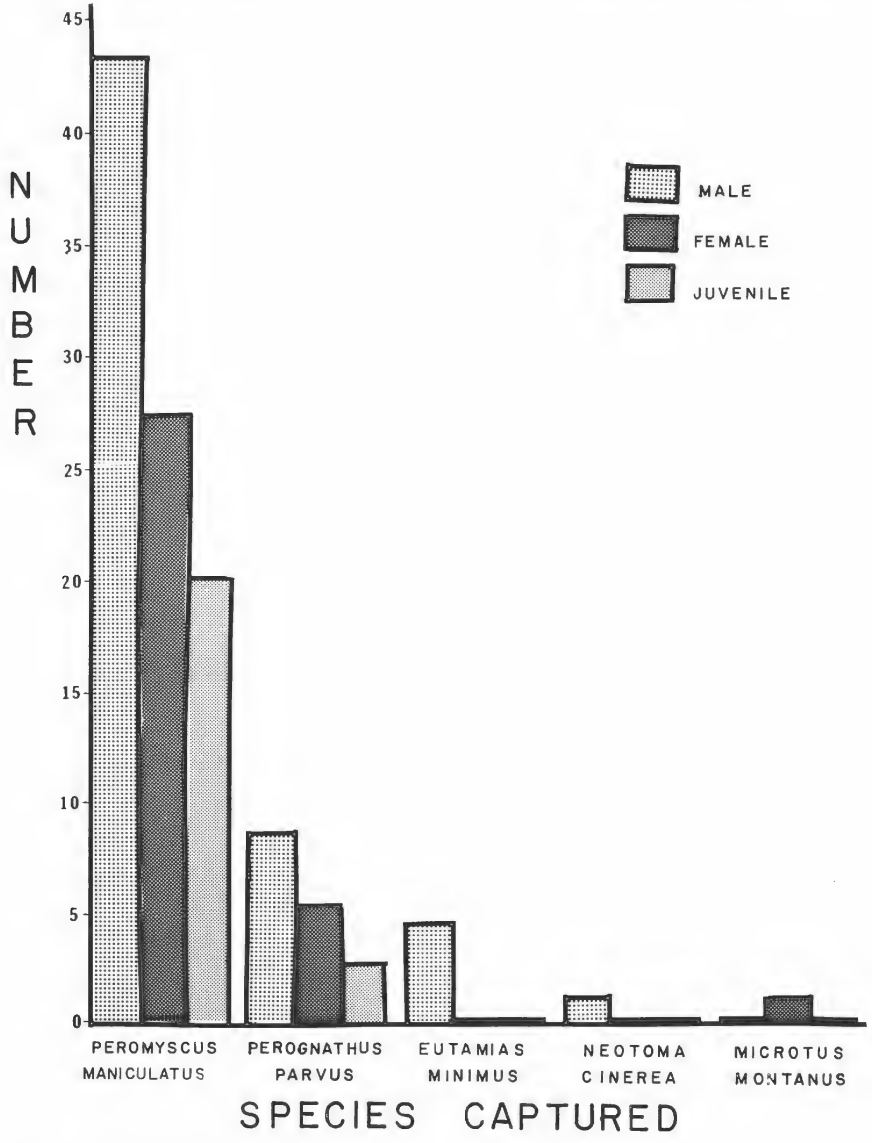

Figure 2. Number and sex of small mammal species captured. Newark Summit.

Discussion

Cronquist *et al.* (1972) consider Newark Summit part of the Central Great Basin floristic section, an area of about 78,347 km^2. More specifically, Billings (1951) classifies this area to be part of the upper sagebrush-grass zone of the Basin Range series. This zone lies above the piñon-juniper belt which marks an increase in elevation on most central Great Basin ranges. Colder climate and more than twice the precipitation of the lower zones is characteristic of the upper sagebrush-grass zone (Billings, 1951). Consequently, greater species diversity as well as increased vegetational cover is found in this zone even though many species found in the lower zones are found here also.

According to Billings (1951), sagebrush is the dominant species of the upper sagebrush-grass zone with several other woody species appearing as co-dominants: *Cercocarpus ledifolius*, *Symphoricarpos vaccinoides*, and *Amelanchier pallida* are examples. A comparison of the relative vegetational coverage or dominance per species for the four lines shows shifting values for the most dominant species along each line segment (Table 1). On line segment 1, ARTR is clearly dominant, with important sub-dominants being PUTR and SYVA. On line 2, ARTR is again dominant— in this case with almost 50 percent of the total relative coverage. PUTR and SYVA are still important sub-dominants but relatively far less so. Grasses and forbs are less frequent. On segment 3, ARTR is still dominant, but CHsp and CHNA are now the important sub-dominants. On line 4, however, ARTR has become sub-dominant to BERE. CHNA and PUTR are important sub-dominants on this line.

In view of BERE and CHNA sub-dominance on lines 3 and 4 and their total absence or relative unimportance on lines 1 and 2, we suggest that some real difference is occurring between the area sampled by line pairs 1-2 and 3-4 with respect to what Cain and de Oliveira Castro (1971) define as a community's "characteristic combination of species." This difference between the two pairs of lines is explained as follows. Both pairs of lines (1-2 and 3-4) are, respectively, geographically separated into two distinct areas by approximately 200 m on opposite sides of a low and gently sloping ridge. Differences in orientation (exposure) and slope also occur (see *Results*). Furthermore, the remarkably consistent percentages of total cover also suggests that lines 1 and 2 are closely associated, as are lines 3 and 4 (Table 1). On a percentage basis, total coverage for line 1 is 62.4; line 2, 65.6; lines 3 and 4 show percentages of 49.1 and 50.4, respectively. These figures indicate that coverage—perhaps even abundance—of plants on lines 3 and 4 is much less than that on lines 1 and 2. We hypothesize that the cover values suggest that the spacing between individual plants is greater on lines 3 and 4 than on lines 1 and 2. A more meaningful analysis of the data might be made through the combination of the line coverage data of lines 1 and 2 as well as line 3 with line 4.

The combined data for lines 1 and 2 still show ARTR to be dominant. PUTR and SYVA are important sub-dominants that have almost equal importance if percentages of coverage are combined. Forb and grass cover for lines 1 and 2 combined constitutes 22 percent of the total cover. The combined data for lines 3 and 4 also show ARTR to be dominant, but to a significantly lesser extent than on lines 1 and 2. CHNA is an important sub-dominant on lines 3 and 4, as are BERE and CHsp. For these two lines, forbs and grasses represent 16.2 percent of the total coverage. Comparison of lines 1 and 2 with 3 and 4 reveals an important change in composition and dominance in the plant communities. ARTR, PUTR, SYVA, and forbs hold the four highest dominance

values on lines 1 and 2; but on lines 3 and 4, ARTR, CHsp, BERE, and CHNA are dominants. Apparently this comparison of line pairs shows that there is a definite difference in community structure between the two areas sampled by lines 1 and 2 and lines 3 and 4.

Figure 1 shows data by plot for shrubs by species and forb/grass. ARTR is again the dominant woody species with total coverage of 23.4 percent. Sub-dominants SYVA and PUTR ranked second and third with 8.22 percent and 6.73 percent total coverage, respectively. The difference in coverage previously noted among the line segments is not obvious here. Instead, four or five plots are within one standard deviation of the mean of 63.33 percent. However, average percent of coverage for all plots (63.33) and all line segments (59.3) is similar. We explain this discrepancy in plot vs line data by the non-random placement of plots along randomly directed line segments. At the start of this project, we decided that although the line starts from a randomly selected point, plots would be placed at 200 m intervals along the line to maintain consistency. Further, we question the adequacy of five plots to represent accurately the vegetation sampled by 1000 m of line intercept. If only one plot falls in an unusual area the total plot data are more greatly affected than if only 10 m of line passes through this same area. Consequently, in further segments of this study, plot data will not be weighted equally with line intercept.

Many factors acting alone or in combination could be the cause of the apparent difference in community structure noted previously. The answer to this variation could lie in basic ecological concepts such as Liebig's law of the minimum and Shelford's law of tolerance. Environmental factors could include variances in soil texture, composition, nutrients, and pH; or slope and exposure of the site and their subsequent influence upon moisture conditions (Odum, 1971; Wyckoff, 1973). We suggest that in this study, moisture variability alone is probably the most important factor affecting variability of species present. Further, we note that slope and exposure (and their parallel effects on soil moisture) are important at this site. Lines 1 and 2 transected a natural wash, whereas lines 3 and 4 were on a high desert plain. This difference would suggest important water availability differences between the micro-ecosystems which would lead to a consequent difference in vegetation. These differences are then further reinforced by grazing patterns, with the animals tending to graze where food is most available. Young *et al.* (1972) and Piemeisel (1951) state that plant communities in the Great Basin are susceptible to invasion by alien annual species. These annuals have highly developed breeding systems which permit adaptation to changing environments. Heavy grazing in the Newark Summit area, particularly in the natural drainage topography of line segments 1 and 2, would result in a sufficiently altered environment to permit an abundance of alien annuals. Although the forb and grass cover of lines 1 and 2 seems high, this cover is largely composed of alien species which, according to local ranchers, are not palatable to livestock. The decrease in quality of grazing forage led to the Bureau of Land Management's decision to close this area until native species could recover.

These community differences are also reflected in the small mammal populations. Although only small differences in total number of species captured were observed between the two line groups and among the lines, we believe the grouped differences with respect to total animals captured are important. A critical factor affecting small mammal

populations is the availability of forbs and grasses (Lugaski *et al.*, 1979; Vreeland *et al.*, 1978). Our data support this finding. Of the 45 animals captured, 27 (60 percent) were taken from lines 1 and 2. On a relative basis (adjusting for differences in line length), lines 1 and 2 contain 63 percent of the forbs and grasses. One can compare the mammal plot data with the forb/grass line cover since plot 1 was located on line 1 and plot 2 on line 2. Sixty-seven percent (44) of the total mammals caught in the plots were from plot 1. Of the total forb/grass cover on lines 1 and 2, 60.3 percent was found on line 1. Conversely, half the number of mammals (22) were trapped in plot 2 with the significantly lower grass/forb cover. These findings also confirm the importance of forb/grass cover with respect to small mammal populations. Of relevance is that total plant cover for these two lines is almost identical (62.4 percent and 65.6 percent, respectively). Although these comparisons seem important, we have too few data to test their statistical significance.

The number of each small mammal species captured, separated by sex and by juvenile stage, is shown in Figure 2. According to Hall (1946), the least chipmunk (*Eutamias minimus scrutator*) should be an indicator of the sagebrush zone. ARTR dominance is confirmed by the botanical analysis. The deer mouse (*Peromyscus maniculatus sonoriensis*) is a ubiquitous species whose population numbers are dependent upon community type and competition from other mammals within that community (Hall, 1946; Larrison, 1967). *Perognathus parvus olivaceus* is found in the arid, shadscale zone and to the montane piñon-juniper zone. The meadow mouse (*Microtus montanus microtus*) is typically found in a meadow environment close to water. The nearest water to the study site was .75 km north. The spring discharge was minimal, with a runoff area of about 12 m^2. The bushy-tailed packrat (*Neotoma cinerea*) is an indicator of a Transition to Hudsonian life zone (Hall, 1946).

This unusual collection of animal species may be explained by the vegetation diversity, topography, altitude, and climate. *Peromyscus*, *Perognathus*, and *Eutamias* are common to a typical sagebrush community. Since this upper sagebrush-grass zone is at 2286 m and above the piñon-juniper belt, the climate is not as arid as a similar community found below that belt. At lower elevations in a sagebrush community, *Perognathus* would be dominant because it is characteristically better adaptive to arid conditions. *Peromyscus* would normally be sub-dominant. However, because of the higher precipitation at this elevation, *Perognathus* loses this advantage and the larger, more aggressive *Peromyscus* becomes dominant. Greater precipitation could also account for the occurrence of the more water dependent *Microtus*. In the drier sagebrush communities, one normally finds the desert packrat (*Neotoma lepida*). With an increase in elevation, 2286 m or above, the desert species is replaced by the bushy-tailed packrat, *Neotoma cinerea* (Brown, 1971). The occurrence of this *Neotoma* species is currently regarded as replacement reflecting altitudinally induced habitat change.

Conclusion

Area 3 is best described as a high sagebrush-grass community in the Basin Range series as so classified by Billings (1951). Apparently, our slightly dichotomous findings have come about as a result of the intensive grazing pressure on this area in recent years. Intensive study such as this could present a powerful management tool as an aid in decision making relative to grazing of public lands. We suggest that an analysis of the vegetation

community is a good indicator of animal species and their population sizes. Our methods must be further tested to determine whether they are valid measures of plant and animal interactions.

Acknowledgments

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Appendix

A. Plant Presence List with Woody Species Abbreviations.

Shrubs

Species	*Abbreviation*	*Species*	*Abbreviation*
Amelanchier pallida	AMPA	Petrophytum caespitosum	PECA
Artemisia tridentata	ARTR	Prunus vibginiana	PRVI
Berberis repens	BERE	Purshia tridentata	PUTR
Chamaebatiaria millefolium	CHMI	Ribes cereum	RICE
Chrysothamnus nauseosus	CHNA	Rosa woodsii	ROWO
Chrysothamnus sp.	CHsp	Sambucus microbotrys	SAMI
Chrysothamnus viscidiflorus	CHVI	Symphoricarpos parishii	SYPA
Leptodactylon pungens	LEPU	Symphoricarpos vaccinoides	SYVA
Lygodesmia spinosa	LYSP	Grass/forb	GRFO

Trees

Species	*Abbreviation*	*Species*	*Abbreviation*
Cercocarpus ledifolius	CELE	Pinus monophylla	PIMO
Juniperus osteosperma	JUOS		

Grasses

Species	*Species*
Agropyron sp.	Oryzopsis hymenoides
Elymus cinereus	Stipa comata
Bromus tectorum	

Forbs

Species	*Species*
Achillea lanulosa	Eriogonum umbellatum
Agastache urticifolia	Grindelia squarrosa
Argemone munita rotundata	Ipomopsis aggregata
Astragalus sp.	Iva axillaris
Calochortus nuttallii bruneaunis	Lithospermum ruderale
Camelina microcarpa	Lupinus sp.
Castilleja sp.	Machaeranthera canescens
Cirsium utahense	Penstemon sp.
Collomia grandiflora	Petradoria pumila
Convolvulus arvensis	Senecio multilobatus
Crepis acuminata	Sidalcea oregana
Erigeron sp.	Sphaeralcea ambigua
Erigeron bloomeri	Urtica holosericea

B. Vertebrate Species Presence List.

Mammals

Canis latrans lestes (coyote)
Eutamias minimus scrutator (least chipmunk)
Microtus montanus microtus (montane meadow mouse)
Neotoma cinerea (bushy-tailed packrat)
Odocoileus hemionus hemionus (deer)
Perognathus parvus olivaceus (pocket mouse)
Peromyscus maniculatus sonoriensis (deer mouse)

Reptiles
Crotalus viridis lutosus (great basin rattlesnake)
Sceloporus magister (desert spiny lizard)
Birds
Alectoris chukar (chukar)
Amphispiza belli (sagebrush sparrow)
Aquila chrysaetos (golden eagle)
Corvus corax (raven)
Sialia currucoides (mountain blue bird)

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Some Implications of Sediment Studies for Glacial Erosion on Mount Rainier, Washington

Abstract

A study of glacial sediments throws light on rates and mechanisms of glacial erosion on Mount Rainier, Washington. Suspended-sediment transport measurements suggest that most of the Nisqually River's suspended-sediment load has been entrained by the time the stream emerges from beneath the terminus of Nisqually Glacier. Calculations of the englacial- and superglacial-debris loads of Nisqually Glacier indicate that more than two-thirds of the stream sediment must be derived subglacially. Lithologic composition of outwash and theoretical considerations also suggest that valley glaciers on Mount Rainier have exceptionally high subglacial erosion rates.

Introduction

During a study of glacial sediments on and near Mount Rainier, Washington, I made a number of observations that bear on the rates and mechanisms of glacial erosion. Some of these have been discussed in a previous paper (Mills, 1976); additional findings are discussed herein.

Mount Rainier (lat 46° 52′ N, long 121° 46′ W) is a Quaternary andesitic stratovolcano in the Cascade Range that rises to an elevation of 4392 m. The main cone rests upon granodiorite of the Miocene Tatoosh pluton and to a lesser extent upon older Tertiary volcanic and volcaniclastic rocks. Nisqually Glacier, a 7-km long valley glacier on the south flank of the mountain, is by far the most intensely studied glacier on Mount Rainier. Its steep longitudinal gradient averages 30° above the equilibrium line (E. L.) (elevation about 2300 m) and 14° below. Ablation rates are high, reaching 8 m/yr near the terminus. Hodge (1972, 1974) showed that the glacier is thin and fast-moving. He found the ice thickness to average about 70 m in the ablation zone; a steeper surface slope indicates the ice is even thinner in the accumulation zone. He determined the centerline surface velocity to range from 160 m/yr near the E. L. to about 30 m/yr near the terminus. He calculated that basal sliding accounted for 90 percent of the movement near the E. L. and nowhere accounted for less than 50 percent. He also found that the bedrock floor of the glacier is quite irregular; coupled with the steepness of the ice surface, this fact explains the highly crevassed nature of the glacier. Other valley glaciers on Mount Rainier probably have similar characteristics.

Nisqually River heads at the terminus of Nisqually Glacier, emerging from beneath the ice as a swift, extremely turbulent meltwater stream. The source and origin of the sediment in this stream constitute the main subject of this paper.

Source of the Stream Sediment

Nelson (1974) estimated the annual suspended-sediment load of Nisqually River at a gauging station near National, Washington (35 km below the terminus of Nisqually

Glacier) to be about 300,000 t (tonnes) yr. In order to use these data to calculate erosion rates on Mount Rainier, it is important to know how much of this sediment is produced by modern erosional processes on the volcano. The problem is summarized in Figure 1. Basically, there are three possible sources of sediment. First, sediment derived from present-day erosion of Mount Rainier may be carried directly to the gauging point via the meltwater stream (path A in Fig. 1). An individual particle may be deposited on the floodplain and subsequently re-entrained several times during its journey, but the average transit time should be relatively short, probably on the order of decades. Second, sediment may be carried away from the volcano by processes such as glacial advances, lahars, and rock falls. These processes often deposit sediment some distance from the floodplain, so that a given particle may not find its way into the stream and thence to the gauging point for thousands or tens of thousands of years (path B in Fig. 1). Third, sediment may be derived from sources unrelated to Mount Rainier (path C in Fig. 1). Based upon certain assumptions (Mills, 1976), it has been estimated that of the 300,000 t/yr of suspended sediment reaching the station at National, 278,000 t/yr can be attributed to modern-day erosion on the volcano (path A) or to erosion of Neoglacial drift within 2 km or so of the glacier termini (path B). Because this 278,000 t/yr is contributed by three meltwater streams of roughly comparable size (Nisqually River, Kautz Creek, and Tahoma Creek, the latter two being tributaries of the former), approximately one-third of this amount, or about 90,000 t/yr, is probably contributed by the uppermost Nisqually River itself. In the present study an attempt was made to check this 90,000 t/yr estimate by actual measurement, and also to see whether path A or B is the more important.

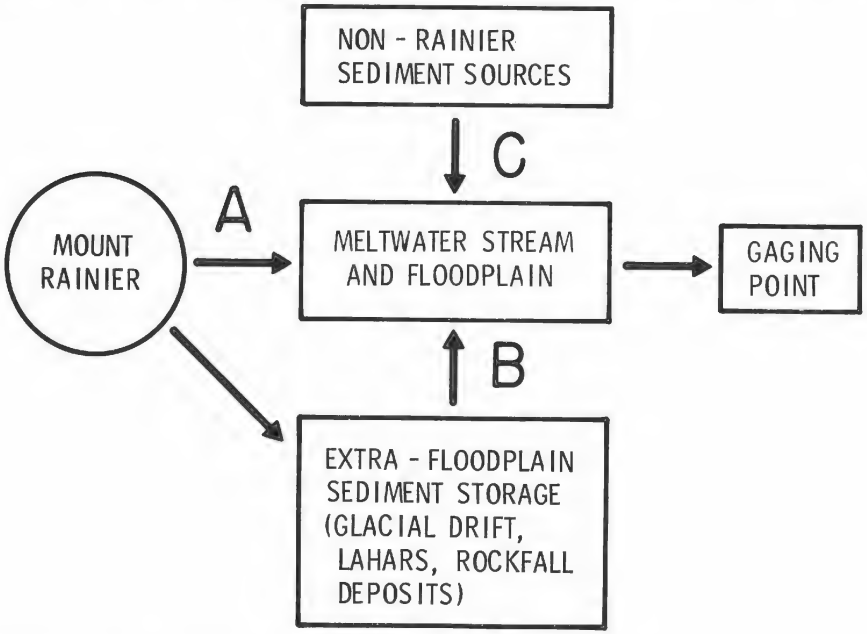

Figure 1. Possible sources of suspended sediment in Nisqually River.

Between 15 May and 1 August 1976, 20 suspended-sediment samples were collected and the stream discharge measured at a point 1.8 km below the Nisqually Glacier terminus. A linear regression of the log of sediment concentration on the log of discharge was performed, giving the regression equation, $Y=0.188\ X^{1.64}$ (where Y is in parts per million and X is in cubic feet per second). Such a regression line can be used to estimate the annual suspended-sediment yield from a stream hydrograph. Unfortunately, no facilities for continuous discharge recording were available. However, it was possible to construct an approximate hydrograph, and from this description an order-of-magnitude estimate of yield was made. On this basis it was estimated that the upper Nisqually River transported at least 50,000 t during the ablation season (during which most of the annual transport probably occurs, as discharge is low during the remainder of the year). Because of the lack of continuous discharge recording, however, peak discharges probably were omitted, and these might have transported large quantities of sediment. As an example of the importance of rare peak discharges, Østrem and others (1967) found that, for the Decade River on Baffin Island, 60 percent of the total suspended-sediment yield for the entire summer of 1965 was transported in a single day. Thus, the upper Nisqually probably could easily account for 90,000 t/yr.

A second approach to the problem was to determine the downstream variation in suspended-sediment load at a given instant in time. This calculation was done by near-simultaneous sampling and measuring of stream discharge at three points, one at the glacier terminus, one 1.8 km below the terminus (near the downstream limit of Neoglacial drift), and another 4.9 km below. By their locations it can be inferred that sediment collected at the upper station was derived mainly via path A (Fig. 1); that at the middle station was derived via path A plus B (the latter being confined to erosion of Neoglacial drift); and that sediment at the lower station was derived via path A, B, and C.

Results are presented in Figure 2; points along a vertical line represent simultaneous samples. Only three samples were taken at the upper station, and because of extreme turbulence no discharge measurements were made there; instead, discharge was estimated to be 0.75 times that at the middle station. Figure 2 shows that early in the ablation season, sediment transport rates 4.9 km below the terminus were slightly greater than at 1.8 km below, although rates were very low in both cases. With the beginning of high discharges in early July, however, in every case the sediment load at the lower station was actually *less* than the load at the middle station; in other words, not only was no additional sediment entrained in the reach between these stations, but sediment was actually lost. This sediment appeared to be deposited in slack water, especially in the lee of boulders at the edge of the stream. Since there is no evidence of long-term aggradation of fines, it may be that this deposition is temporary; perhaps during large floods this material is entrained. This result implies that most suspended sediment is supplied either by the glacier itself or by erosion of Neoglacial drift, as suspected earlier. A comparison of samples at the upper and middle stations suggests that of these two latter sources, that supplied by the glacier is by far the more important, as the sediment load either decreases or shows only a slight increase over this 1.8-km reach. Because only three samples are involved, however, this conclusion must remain highly tentative until additional data are available.

No mention of bedload has been made. Fahnestock (1963) demonstrated that bed-

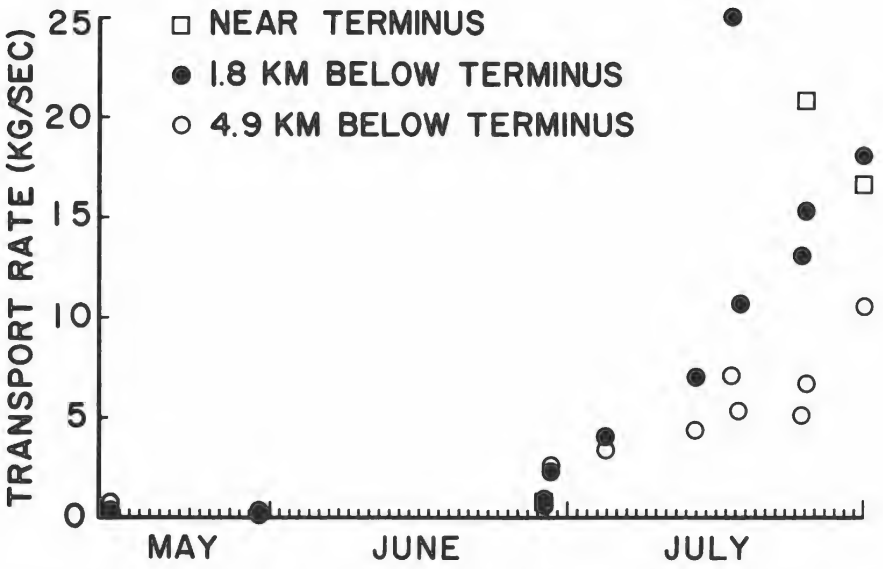

Figure 2. Suspended-sediment transport rates at three stations on upper Nisqually River, as determined by near-simultaneous sampling.

load transport rates below Emmons Glacier on Mount Rainier can be quite high, and no doubt during occasional floods they are high on the Nisqually River, too. However, except for immediately below the terminus, little movement of bed material was detected (either aurally or by contact while wading) during the summer of 1976. Thus, it appears that suspended sediment accounts for the bulk of sediment transport in the stream.

Origin of the Sediments

The above evidence suggests that the meltwater stream has entrained most of its suspended sediment by the time it emerges from beneath the glacier. It is therefore necessary to look above the glacier terminus for the origin of this sediment. Two questions arise: the first involves the ultimate source of the rock debris; the second, the manner in which this debris is transported by the glacier. In response to the first question, there are basically two potential sources for debris: rockfall and subglacial erosion. Rockfall is exceedingly common on the high, unstable walls that flank the upper end of the glacier; the efficacy of subglacial erosion is more difficult to determine. The answer to the second question depends to a large extent on the thermal regime of the glacier. According to Boulton (1972), in warm-based glaciers the debris produced by subglacial erosion is confined mainly to a basal layer of ice no thicker than 1.0 m; it rarely finds its way into englacial or superglacial positions, even in the ablation zone where flow lines have an upward component. If deposited, such debris is deposited as lodgment till. In cold-based glaciers, however, particularly where water can reach the bottom and refreeze there, subglacially derived debris may be carried to high levels in the ice and much of it may end up as englacial or superglacial debris.

Because Mount Rainier lies in a maritime climatic zone, one would expect its glaciers

to be essentially warm based. This expectation would imply, according to Boulton's (1972) model, that the impressive superglacial-debris mantles visible in the ablation zones of Rainier valley glaciers late in the summer are probably derived from rockfall. Apparently much of this rockfall takes place above the E. L. and is incorporated into the ice as englacial debris, eventually melting out below the E. L. to form superglacial debris. In at least some cases, however, it appears that a substantial portion of the superglacial debris must be subglacially derived. For example, Winthrop Glacier on the north slope of Rainier has no headwall and is flanked by relatively low walls, yet even the center of the glacier displays a large amount of superglacial debris at its lower end; this debris, at least, must be subglacially derived. This observation probably does not contradict Boulton's (1972) model, however. Because of Mount Rainier's high elevation, it seems quite likely that the upper ends of the valley glaciers are cold based. Miller (as cited in Kiver and Steele, 1975) measured temperatures of -10° C in a snowpit near the summit, and the upper ends of the glaciers must be nearly as cold. Furthermore, the thin, highly crevassed ice in the upper reaches of the glaciers probably allows significant meltwater to reach the glacier base where it refreezes and thus promotes basal plucking.

Cold ice is probably limited to the highest reaches of the glaciers and is almost certainly not found below the E. L. Hence, although subglacially derived debris may be carried into englacial positions in the upper end of the glacier, it is likely that below the E. L. little additional englacial or superglacial debris is derived from the glacier base, even though basal erosion by abrasion and crushing is probably quite effective here. Thus, debris is carried through the ablation zone in two separate, relatively independent systems: the englacial/superglacial system and the basal system. This model is assumed in the following discussion.

If two simplifying assumptions are made, it is possible to make a rough estimate of the superglacial/englacial debris transport rate by using cross sections and centerline surface velocities of Nisqually Glacier determined by Hodge (1972, 1974) and measurements of average superglacial-debris thickness on the same glacier made by me. The transport rate of basal debris can then be estimated indirectly by subtracting this rate from the sediment-transport rate of the upper Nisqually River.

The first assumption is that englacial debris in the ablation zone has a fairly uniform distribution in the ice. My observations have revealed no debris bands or other high concentrations of sediment in the glacier. Instead, debris appears to be rather diffusely dispersed throughout the ice. In addition, the concentration of debris appears to be just as great in the upper layers of the ice as in lower layers (excepting the thin basal layer). The second assumption involves the fact that Hodge (1972, 1974) measured only the centerline surface velocity. Obviously the use of the latter in the calculations discussed below overestimates the average flow velocity through a glacier cross section, both because surface velocities near the edges will be lower than those near the centerline and because velocities at depth will be lower than those at the surface. However, because of certain characteristics of Nisqually Glacier, it is assumed that centerline surface velocity does not exceed average velocity by more than a factor of about two. There are two reasons for this assumption. First, the cross sections in the upper part of the ablation zone are different from the usual parabolic cross sections of many valley glaciers in that the ice at the centerline is not greatly thicker than elsewhere across the glacier width. Because depth is one of the main controls of velocity, the surface velocities across a large

part of the total glacier width are thus likely to be not greatly less than the centerline surface velocity. Second, concerning the decrease of velocity at depth, basal sliding is estimated to account for 90 percent or more of the surface velocity in the upper ablation zone (Hodge, 1972), so that the difference between surface velocity and velocity ablation over depth must be small. Even in the lower ablation zone basal sliding accounts for at least 50 percent of the surface velocity (Hodge, 1972), so that surface and average velocity should still be of the same order of magnitude. In any event, transport rates calculated on the basis of centerline surface velocities can be regarded as maximum values.

Given the above assumptions, the following procedure was used to calculate the transport rate of superglacial and englacial debris. In order to determine rates for superglacial debris alone, the thickness of the debris mantle was first determined at a number of points along profiles C8 and C2 (Fig. 3) by digging pits; the average thicknesses obtained were 21 cm and 48 cm, respectively. By multiplying the average debris thickness by the glacier width at each profile and by then multiplying this product by the velocity in m/yr (centerline surface velocities are given in Fig. 3), the annual discharge of superglacial debris past each profile was calculated. Results show that 7560 m^3 of superglacial debris is carried past C8 annually and 4320 m^3 past C2. The latter value must be corrected for the fact that the glacier bifurcates above C2 as shown in Figure 3. Cross section C6 shows that only about two-thirds of the glacier is represented by the west

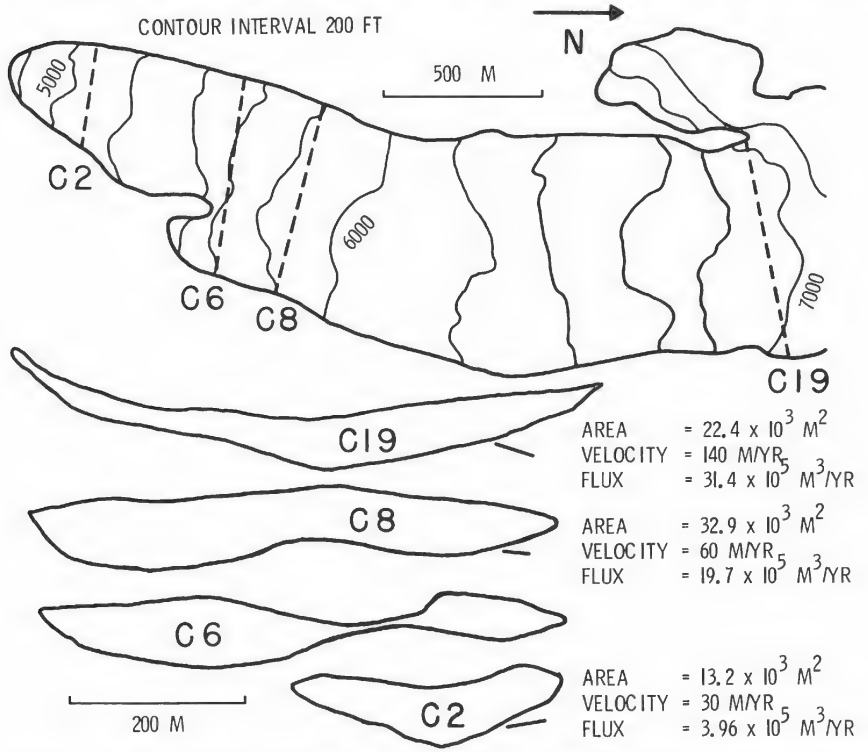

Figure 3. Ice fluxes through representative cross sections of lower Nisqually Glacier (velocities and cross sections from Hodge, 1972). Cross sections are drawn looking downglacier.

prong where C2 is located, so that the superglacial debris discharge at C2 should be multiplied by 1.5 to account for debris carried into the east prong, thus making the results equivalent to those at C8; this calculation gives an annual discharge of debris at C2 of 6480 m^3. The fact that the discharge of superglacial debris *decreases* between C8 and C2 even after this correction has been applied may seem surprising, for much additional englacial debris is released by ablation between these two profiles. The explanation of this phenomenon probably involves loss of superglacial debris as the ice moves downglacier; some of the debris is deposited along the sides of the glacier because of lateral ablation and some falls into crevasses.

In order to estimate the combined englacial/superglacial debris discharge, ice fluxes through C19 and C8 were first estimated by multiplying velocities by the cross-sectional areas at these locations (Fig. 3). C19 is not far below the E. L.; the ice flux through this cross section (31.4×10^5 m^3/yr) represents the total amount of ice passing the E. L. annually. By C8 the ice flux has dropped to 19.7×10^5 m^3/yr, so that between C19 and C8, 11.7×10^5 m^3/yr of ice is lost by ablation. The melting of this much ice, then, releases 7560 m^3 of englacial debris per year (the annual superglacial debris discharge at C8). This figure indicates that the debris concentration of the ablated ice is 0.65 percent by volume, or, assuming a density of 1700 kg/m^3 for the superglacial debris, a concentration by weight of about 11 kg/m^3. To estimate the maximum debris discharge of the glacier, the total ice discharge through the E. L. (where englacial debris has not yet begun to melt out) was then multiplied by this concentration, giving a discharge of about 34,500 t/yr. For reasons discussed above, this estimate is probably a generous one, although the actual value is thought to be not less than half this amount. Certainly 34,500 t/yr can be regarded as a maximum transport rate.

The above calculations indicate, then, that less than one-third of the estimated 90,000 t/yr of sediment supplied to Nisqually River can be accounted for by the englacial/superglacial debris transport system. This finding implies that unless the estimate of 90,000 t/yr is grossly in error, a considerable amount of sediment must be supplied by the subglacial transport system and/or perhaps by subglacial fluvial erosion. Additional evidence that the subglacial load must be important is furnished by a consideration of the particle-size distribution of the sediment transported by the river and that of the superglacial/englacial debris. The greater part of the former consists of suspended-sediment which, as analysis of three samples showed, is confined almost completely to particles less than 2 mm in size. In contrast, a number of size analyses of superglacial debris (performed by using field point-counting for particles larger than 102 mm and sieving for smaller particles) showed that only 16 percent of this material consisted of particles less than 2 mm. Where does all the fine material come from? One possibility investigated was that englacial debris might contain a much higher percentage of fines than does the superglacial debris, the fines being carried away to the meltwater stream during the melt-out process. To test this possibility, two samples of ice were collected, allowed to melt, and the particle-size distribution of the released englacial debris then compared with that of superglacial debris samples collected at the same sites. The results showed that englacial debris is only a few percent higher in silt and clay than superglacial debris.

Another possibility is that the fines are winnowed out of the glacial debris, leaving behind the larger particles. However, because the glacial debris contains only 16 per-

cent of material fine enough to be carried as suspended sediment, in order to obtain the estimated annual load of 90,000 t/yr, it would be necessary to winnow 560,000 t/yr of this debris, even if 100 percent of particles less than 2 mm were entrained. In actuality, size-distribution analyses of outwash show that winnowing is somewhat less efficient than this, so that it would be necessary to winnow well over 1,000,000 t/yr to obtain the 90,000 t/yr of suspended material. Obviously, winnowing can explain only a small part of the suspended load.

The most probable origin of the fine material is that it is produced by abrasion at the base of the glacier. This conclusion is suggested by two considerations. First, many glaciers deposit lodgment till that is subglacially derived and contains a large percentage of material less than 2 mm in size (Mills, 1977). For example, lodgment till of nearby Paradise Glacier contains 65 percent particles less than 2 mm. Nisqually Glacier and other large valley glaciers on Mount Rainier, however, display no such tills. A possible explanation for this absence is provided by Boulton (1975), whose calculations show that lodgment should not take place beneath glaciers similar to Nisqually Glacier in thickness and basal sliding velocity. Presumably, material similar to lodgment till is produced beneath Nisqually Glacier, but is released to subglacial meltwater streams rather than being deposited.

In addition, theoretical considerations suggest that the rate of abrasion should be very high beneath Nisqually Glacier. Several factors affect the efficacy of subglacial abrasion. First, the velocity of basal sliding is quite important (Boulton, 1974), so that Nisqually Glacier, with a basal sliding velocity of up to 144 m/yr, should be highly effective in this regard. Second, Röthlisberger (1968) has pointed out that continual movement of rock particles toward the bed is important in order to renew the abrasive material constantly, and concluded that the most effective way for this renewal to occur in a warm-based glacier was by melting of the basal ice. Several conditions should produce exceptionally high rates of basal melting beneath Nisqually Glacier. First, the geothermal heat-flow rates have been shown to be quite high near the summit of Mount Rainier (Kiver and Steele, 1975); possibly they are also high, at least locally, beneath the glaciers on the mountain's flanks. Second, basal sliding produces heat that results in basal melting (Sugden and John, 1976); hence, a high rate of basal sliding produces high rates of basal melting. Third, because of the high rate of surface melting in the ablation zone (8 m/yr) and because of the thin, highly crevassed nature of the glacier, exceptional amounts of meltwater undoubtedly reach the base of the glacier and thereby greatly increase basal melting.

A third factor promoting abrasion is a thin ice cover. According to Boulton's (1975) calculations, for example, when the basal sliding velocity is 100 m/yr, abrasion rate is at a maximum when effective normal pressure is between 10 and 30 bars (ice thickness between 90 m and 270 m, assuming zero water pressure). Above 30 bars, abrasion rate decreases rapidly because friction between the bed and rock particles embedded in the glacier sole becomes sufficiently great to retard the movement of the particles. Below a pressure of 10 bars abrasion rate also decreases, but even at a pressure of 5 bars (45 m of ice) the abrasion rate is near maximum. For most glaciers, then, abrasion is effective only near the ice margin. For Nisqually Glacier, which probably is rarely much thinner than 45 m and never thicker than about 90 m, abrasion rates should be near maximum beneath much of the glacier length.

A consideration of the lithologic composition of clasts in the outwash provides evidence that erosion beneath Rainier valley glaciers also produces a substantial amount of coarse material. The lower ends of the valley glaciers on Mount Rainier have cut through the Rainier andesite and now rest upon pre-Rainier formations; hence, clasts composed of pre-Rainier lithologies presumably are basally derived. Thus, by making lithology counts in a deposit, it is possible to place a minimum on the percentage of material that has a subglacial origin.

More than 90 such counts were made. They showed that superglacial debris contained virtually no pre-Rainier rocks at any glacier. Till deposits had little more, thus indicating that for the most part they consist of material derived from the superglacial or englacial environment. Outwash, on the other hand, contained large numbers of pre-Rainier clasts, thus demonstrating the effectiveness of subglacial erosion, at least in the ablation zone. The percentages of such clasts in outwash varied somewhat from glacier to glacier, however. In an effort to determine the reason for this variation, the maximum percentage of pre-Rainier clasts in four meltwater streams (as measured just below the glacier termini) were related to several possible determining factors (Table 1). The first factor is type of pre-Rainier bedrock; theoretically, the less-resistant Tertiary volcanics might produce more clasts than the more resistant granodiorite. The results (Table 1) indicate this factor is probably not significant, for although Cowlitz-Ingraham Glacier overlies a large area of Tertiary volcanics and has the highest percentage of pre-Rainier clasts, Emmons Glacier also overlies a large area of Tertiary volcanics but has the lowest percentage.

TABLE 1. Possible factors affecting percentage of pre-Rainier rock in Rainier valley-glacier outwash.

Glacier	Percent pre-Rainier clasts in outwash near present terminus	Lithology of pre-Rainier outcrops	Horizontal distance between present terminus and highest pre-Rainier outcrop	Thickness of superglacial debris cover
Nisqually	40	Granodiorite	1.1 km	48 cm
Carbon	20	Granodiorite plus small amount of Tertiary volcanics	5.3 km	100+ cm
Cowlitz-Ingraham	50	Tertiary volcanics plus small amount of granodiorite	2.3 km	7 cm
Emmons	9	Granodiorite and Tertiary volcanics	2.4 km	Greater than Carbon

A second factor is the total area of pre-Rainier bedrock beneath the glacier. Although this area cannot be determined directly, the distance above the terminus of the most upglacier pre-Rainier outcrop adjacent to the glacier margin can be determined, and should correlate roughly with this area. Table 1 suggests that this factor exercises little influence. A third factor is the superglacial debris load of the glacier, which will tend to dilute the basally derived pre-Rainier material in the outwash because in all cases it is nearly 100 percent andesite. As an index of this load, the average thickness of the superglacial debris mantle at a point several hundred meters above the glacier terminus was measured. No measurement of this thickness was made on Emmons Glacier, but as products of the 1963 Little Tahoma Peak rockfall (Crandell and Fahnestock, 1965) were still being delivered to the terminus, it is likely that this glacier had the highest super-

glacial debris load. Table 1 suggests that this factor may be the most important, for the order of increasing percentage of pre-Rainier clasts in the outwash corresponds to the order of decreasing superglacial debris thickness.

Conclusion

Measurements of suspended-sediment transport in the upper reaches of Nisqually River indicate that the bulk of suspended sediment in the river is entrained at or above the glacial terminus. Calculations of the englacial/superglacial debris load of Nisqually Glacier suggest that less than one-third of the stream sediment can be attributed to these sources, so that the remainder must be derived subglacially. Natural tracers in the outwash as well as theoretical considerations support the idea that subglacial erosion rates are exceptionally high beneath valley glaciers on Mount Rainier.

Although more data are needed before firm conclusions can be drawn, the results bear on the question of what magnitude of suspended-sediment loads can be expected during the next several decades in the lower reaches of meltwater streams draining Mount Rainier. In an earlier paper (Mills, 1976), I suggested that present suspended-sediment loads may be abnormally high because twentieth century glacier recession has exposed large amounts of loose, unstable drift that is readily entrained by streams; as recession has ceased and newly exposed drift is becoming stabilized, sediment supplied to the streams via path B (Fig. 1) can be expected to decline. However, the present study suggests that sediment derived via path A (modern erosional processes on Mount Rainier) is much more important than that derived via path B. Hence, suspended-sediment loads are unlikely to decrease significantly in the near future.

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Vegetation Mapping and Community Description of a Small Western Cascade Watershed

Abstract

Watershed 10 is a 10.24 ha watershed previously used as an intensive study site by the Oregon Coniferous Forest Biome project of the US/IBP (International Biological Program). Through the use of an established trail and grid system as well as a stem map of all trees greater than 15 cm dbh, 414 individual map units of plant communities were delimited. These were grouped into seven plant communities and four habitat types. I map and describe structural vegetation characteristics of these communities for the entire watershed.

Introduction

Comprehensive studies of ecosystem processes, such as nutrient and carbon flow and cycling, require thorough basic biological and physical descriptions of the system. The need for the basic surveys or descriptions to provide "state variable" data essential to ecosystem modeling efforts is often unappreciated. Even less understood is the potential use of vegetation or plant communities as a basis of stratifying a study area into environmentally and biologically homogeneous "compartments." Such compartments or subareas can be particularly useful when dealing with a diverse tract such as a mountain watershed. Various processes, such as transpiration or photosynthesis, can be simulated separately for each compartment, eliminating the less desirable approach of developing a single average value for an entire, often highly diverse, watershed.

The basic approach used in describing the plant communities and habitat types of Watershed 10 (WS-10) and the resulting descriptions are the subjects of this paper. Watershed 10 was an intensive study site for the Coniferous Forest Biome project of the US/IBP and is the present site for post-logging perturbation studies. The basic vegetation survey was an essential element in determination of standing crops and in indentifying environmentally homogeneous areas within this diverse watershed.

There are several purposes to this paper: first, to document the approach for others faced with similar tasks; second, to provide a historical record of the original vegetation of this watershed which had been clearcut in 1975 as part of further studies; third, to provide quantitative characterization of the composition and structure of an extensive area of old-growth Douglas-fir (*Pseudotsuga menziesii*) forest; and finally, to alert interested scientists to the availability of an accurate stem map of a large, continuous forest area together with the associated stem data set.

Study Area

Watershed 10 is a 10.24 ha watershed located adjacent to the southwestern tip of the H. J. Andrews Experimental Forest (Fig. 1). Elevations range from 430 m to 670 m. Slopes average about 45 percent, but often exceed 100 percent. Soils are classified as

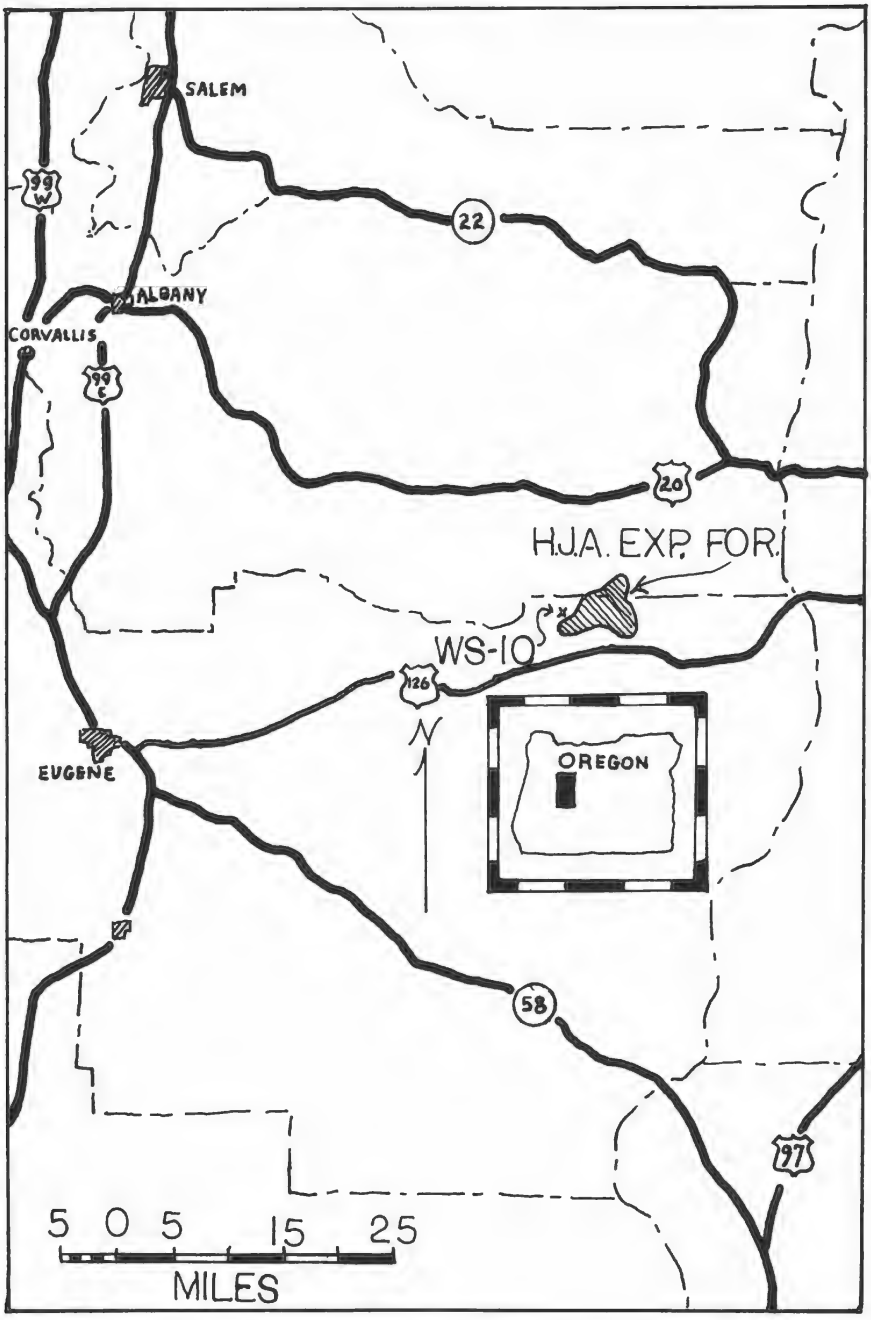

Figure 1. Location of Watershed 10, H. J. Andrews Experimental Forest, central western Cascades of Oregon (Numbers=highway number of highways generally parallel to major rivers).

Typic Dystrochrepts. They typically range from gravelly silty clay loams to very gravelly clay loams, and are derived from volcanic tuff and breccia colluvium parent materials.

Climate is typical of western Oregon Cascades with 2300 mm annual precipitation (75 percent between October and March) and common snow accumulation of short duration. Two years of on-site climatic data show an average daytime temperature of 21°C for July and 0°C for January. Extremes range from 41°C in August to -20° C in December.

Methods and Terminology

Throughout this paper several classification terms are used which need to have their origins and meanings clarified. The classification system presently in use is the Habitat Type system. It is an ecological system which groups similar forest plots into natural and reasonably consistent homogeneous units of climax forest. Habitat types are defined by landform and environmental variables and named by vegetation variables. The lower echelon hierarchical units include the community, which is used as either a general term for discussing different entities or a term which includes a group of stands which are not yet advanced enough to consider as climax. The climax forests are called associations, and each association occurs on a habitat type of the same name. The habitat type includes all land areas capable of supporting stands of any seral stage which demonstrate the potential of developing to a single climax type. A classification key (Dyrness *et al.*, 1974) was used to identify all map units in this study. Several seral communities identified in the key have more than one possible seral direction so that slope, aspect, and landform as well as adjacent vegetation types were used to determine habitat type of seral communities. Seral development of stands in Watershed 10 was considered equivalent to that described by Dyrness *et al.* (1974) for the H. J. Andrews forest.

A slope-corrected 25 m x 25 m grid system was established as a reference system for the entire watershed. Aluminum corner stakes with number tags were installed at each grid corner. All tree stems with a dbh (diameter breast high=1.37 m) $\geq$ 15 cm were mapped, and tagged with sequentially numbered aluminum tags. Data collection included tree species, dbh, location, and notes on the vigor and crown condition. Logs and stumps were also mapped. Logs and stumps are mapped within 2 m of their actual location (Fig. 2).

Vegetation mapping was begun in early summer using a reconnaissance technique (Franklin, Dyrness, and Moir, 1970). Species and cover classes were listed for four strata within each of the 414 reconnaissance map units using an open legend mapping system. The size and shape of each unit were determined by understory plant species and given the community name in accordance with Dyrness, Franklin, and Moir (1974). The four strata include: (1) overstory canopy including mature overstory trees down to a dbh of $\geq$ 15 cm, (2) understory tree stratum including all size classes $<$ 14.9 cm dbh of species which typically attain tree stature in this region and community, (3) tall shrub stratum, and (4) low shrub stratum. Herbaceous species were noted and included in the map symbol in instances where it was felt to be an aid to the final classification of the map unit. Cover was estimated using Daubenmire (1959) cover classes. The major plants of each stratum were listed in order of their cover dominance followed by a single digit indicative of the combined cover class of the stratum. Individual map units were identified and drawn on slope-corrected field maps through the

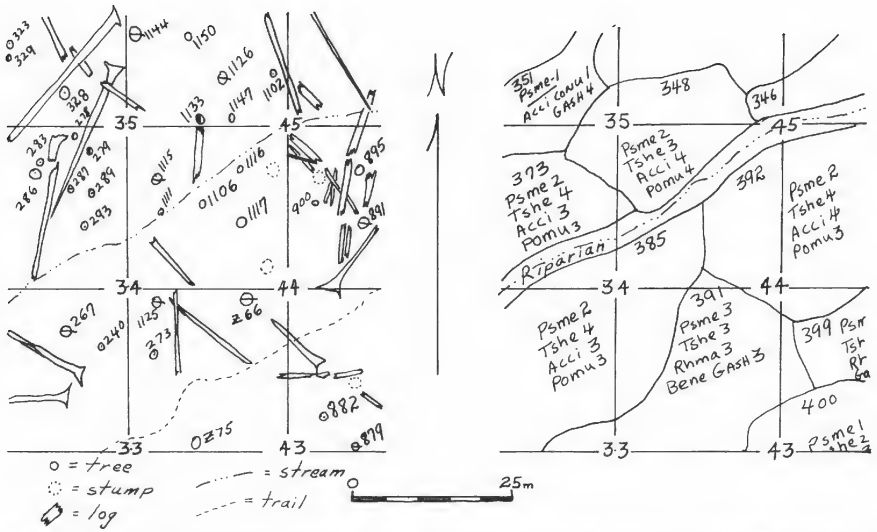

Figure 2. Sample stem map and vegetation unit map of selected grid sections of Watershed 10, H. J. Andrews Experimental Forest.

use of the mapped and tagged trees and the corner post numbers of the grid sections.

The area (in ha) of each of the map units and the percentages of cover within them were calculated with the aid of an electronic grid counting device.

In August 1973, 36 sample plots were established within WS-10 to obtain prelogging data in a study of early succession within habitat types found in the watershed. These successional study plots were placed within previously identified and mapped habitat types in proportion to the percentage of Watershed 10 area occupied by the type. Initial mapping and data from these 36 sample plots have been used as the base data for WS-10 prelogging plant community descriptions.

The sample plots were rectangular, 15 m x 10 m in dimension, slope-corrected, and oriented parallel to contour. Each plot was permanently located by placing metal corner posts referenced to several tree tags and/or numbered grid corner stakes. Data collection included the following: (1) Trees: canopy cover of mature trees ($\geq$15 cm dbh) estimated by species; total density of conifer saplings ($>$1 m tall$<$15 cm dbh), species density; density of conifer seedlings ($>$1 m tall) within representative subsamples of each plot (15 m by 1 m strip above the top, middle, and bottom lines of each plot = 45 m^2); (2) Shrubs: cover and frequency estimated by line intercept along top, middle, and bottom lines of each plot; (3) Herbs: cover and frequency of herb and moss species estimated within 45 microplots (each 2 x 5 dm rectangles) spaced at 1 m intervals adjacent to and below the top and middle plot lines and above the lower plot line; (4) Other: cover of stone, litter, and mineral soil estimated within each of the 45 microplots; lists made of plant species in each plot; photo points established and photos taken in summer and fall at each plot prior to logging; and 16 selected species were measured for leaf area index and biomass data.

Results

The 414 map units were grouped into seven communities: (1) *Tsuga heterophylla/*

Castanopsis chrysophylla (*Tshe/Cach*), (2) *Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon* (*Tshe/Rhma/Gash*), (3) *Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa* (*Tshe/Rhma/Bene*), (4) *Tsuga heterophylla/Acer circinatum/Polystichum munitum* (*Tshe/Acci/Pomu*), (5) *Pseudotsuga menziesii/Acer circinatum/Berberis nervosa* (*Psme/Acci/Bene*), (6) *Pseudotsuga menziesii/Acer circinatum/Gaultheria shallon* (*Psme/Acci/Gash*), and (7) riparian (Fig. 3). The first six are equivalent to associations and communities of the H. J. Andrews Experimental Forest (Dyrness *et al.*, 1974) and span most of the low-elevation moisture gradient for the western Cascades. The riparian community is in fact a complex of stream-associated vegetation types currently under study (A. Campbell, pers. comm.). Each of the communities or habitat types (HT) is described below and its distribution on WS-10 is shown in Figure 3.

The vegetation map does not show ecotones between communities, although they are present at least to some degree. Observed ecotones between major vegetation types were generally narrow, particularly between the environmentally more extreme communities (*Tshe/Cach* and the *Tshe/Acci/Pomu* communities) and any adjacent community. In some cases the ecotones were several meters wide as in the gradual transitions between seral and climax communities on the same habitat type. Ecotones between the *Tshe/Rhma/Gash* and the *Tshe/Rhma/Bene* habitat types are more subtle than those

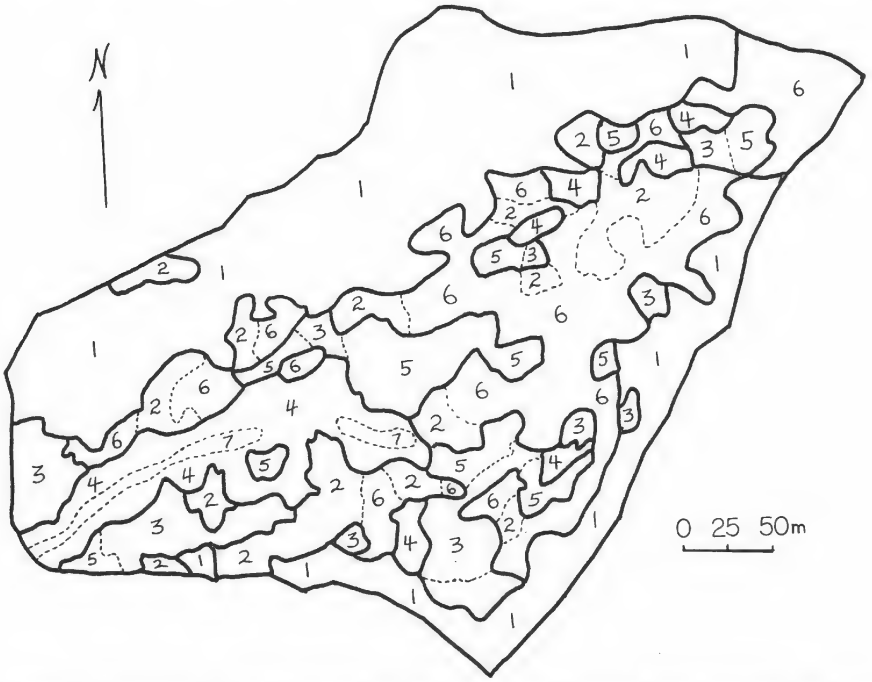

Figure 3. Watershed 10 plant communities (numbered) and Habitat Types (separated by dark lines) (1 = Tshe/Cach; 2 = Tshe/Rhma/Gash; 3 = Tshe/Rhma/Bene; 4 = Tshe/Acci/Pomu; 5 = Psme/Acci/Bene; 6 = Psme/Acci/Gash; and 7 = Riparian communities) (1 = Tshe/Cach HT; 2 + 6 = Tshe/Rhma/Gash HT; 3 +5 = Tshe/Rhma/Bene HT; and 4 + 7 = Tshe/Acci/Pomu HT).

TABLE 1. Diameter size class distribution of trees in Watershed 10 (seedlings and saplings estimated by habitat type subsample).

Size Class (cm)	Species Alpha Code[1] Psme	Tshe	Thpl	Pila	Cade	Cach	Acma	Tabr	Conu	Alru	Arme	Acci
Seedlings (< 1 m tall)	1994	2547	252	448	98	—	—	—	—	—	—	—
Saplings (> 1 m tall < 15 cm dbh)	2596	1965	291	425	5	—	—	—	—	—	—	—
15-30	406	560	65	34	1	518	113	53	26	2	1	1
30-45	94	208	42	11	2	8	15	12	—	1	—	—
45-60	29	64	16	11	2	—	1	—	—	—	—	—
60-75	37	15	8	4	2	—	—	—	—	—	—	—
75-90	53	4	5	3	—	—	—	—	—	—	—	—
90-105	82	4	—	2	2	—	—	—	—	—	—	—
105-120	119	—	2	2	—	—	—	—	—	—	—	—
120-135	88	—	—	2	—	—	—	—	—	—	—	—
135-150	58	—	—	—	—	—	—	—	—	—	—	—
150-165	19	—	—	—	—	—	—	—	—	—	—	—
165+	8	—	—	—	—	—	—	—	—	—	—	—
Total seedlings + saplings	4590	4512	543	873	103	—	—	—	—	—	—	—
Total trees	993	855	138	69	9	526	129	65	26	3	1	1

[1]Psme=**Pseudotsuga menziesii**; Tshe=**Tsuga heterophylla**; Thpl=**Thuja plicata**; Pila=**Pinus lambertiana**; Cade=**Calocedrus decurrens**; Cach=**Castanopsis chrysophylla**; Acma=**Acer macrophyllum**; Tabr=**Taxus brevifolia**; Conu=**Cornus nutallii**; Alru=**Alnus rubra**; Arme=**Arbutus menziesii**; Acci=**Acer circinatum.**

between either of these two communities and the *Tshe/Cach* or the *Tshe/Acci/Pomu* community. Mapping at small scale, the ecotones could easily be drawn on WS-10 maps, but they would be of little use in the context of intended uses of the map.

Basically, WS-10 was a mixture of old-growth and second-growth stands occurring on a mosaic of substrates. This variability in soil depth, slope, and aspect explains in part the mixing of climax communities such as the *Tshe/Cach*, *Tshe/Rhma/Bene*, *Tshe/Rhma/Gash*, and the *Tshe/Acci/Pomu* associations with seral forest stands such as the *Psme/Acci/Gash*, *Psme/Acci/Bene*, and portions of the riparian communities. Fire history has undoubtedly played an important role in the formation and development of plant communities within WS-10, as have bark beetles and windthrow.

Slope and aspect affect plant community development through their effect on stand history; for example, fires, which are known to be a continual source of disturbance in WS-10, tend to be both more likely and more intense on southerly aspects. Fires also have a greater total effect on steep slopes than on gentle slopes. Past disturbance, erosion, and deposition yield differences in soil depth and quality. The result is a watershed with a mosaic of different age classed forests having complex historic involvement in species distribution and structure.

A complete listing of WS-10 trees includes 2815 stems $>$ 15 cm dbh and 12 species as of the summer of 1974 (Table 1). The size class distribution for *Pseudotsuga menziesii* has a biomodal distribution with peaks in the 10 to 40 cm dbh and 80 to 120 cm dbh size class ranges. Factors responsible may include inequalities in growth rates of the trees, slow invasion of WS-10 by *Pseudotsuga*, and periodic creation of small openings by disturbance factors. Disturbance is followed by a gradual successional invasion of *Pseudotsuga.* A preliminary stage structure analysis of WS-10 shows much more age variation than has been suspected for old-growth Douglas-fir forests.

The size class distribution of *Tsuga heterophylla* has the expected J-shaped curve of a climax tree species. The size class distribution of *Thuja plicata* indicates that this species was increasing in numbers in at least some communities and was already an important late seral species. *Acer macrophyllum* apparently does well in earlier stages of secondary succession, but competes poorly with conifers in older stands.

The only other trees which occurred in large numbers in WS-10 were *Castanopsis chrysophylla* and *Pinus lambertiana. Castanopsis* is a hardwood that does not generally attain a very large dbh; 518 of 526 trees in WS-10 were in the 15-30 cm dbh category. *Pinus lambertiana* occurred in a variety of size classes in WS-10 and is generally restricted to the more exposed sites. It was frequently found in the *Tshe/Cach* habitat type and other environments supporting numbers of *Pseudotsuga menziesii* in small as well as large size classes.

Reproductive size classes were well represented in WS-10 with an estimated 10,261 stems. The bulk of them (9102) were *Pseudotsuga menziesii* or *Tsuga heterophylla* (Table 2). Table 2 lists reproduction in stems per hectare in order to derive the relative importance of different species in different habitat types. *Pseudotsuga menziesii* is more common in the drier habitats, particularly the *Tsuga heterophylla/Castanopsis chrysophylla* and the *Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon* habitat types. *Tsuga heterophylla* and, to a lesser extent, *Thuja plicata* were relatively more important in the more mesic habitat types.

In general, the distribution of tree species with different ecologic roles strengthens

the vegetation stratification of the watershed. Peculiarities exist in that *Pseudotsuga menziesii* is reproducing in fairly large numbers over a wider range of the hypothesized moisture gradient (Dyrness *et al.*, 1974) than is typical. This apparent anomaly is probably the result of sampling, since study plots were placed (where reproductive size classes were all estimated) within habitat types in order to sample the variation in the canopy cover of each type. Therefore, open stands were sampled in each habitat type. It was the open stands which included large portions of the *Pseudotsuga menziesii* reproductive size classes.

TABLE 2. Conifer reproduction within four habitat types on Watershed 10 (stems per ha).

Habitat type		Species									
		Pseudotsuga menziesii		**Tsuga heterophylla**		**Thuja plicata**		**Pinus lambertiana**		**Calocedrus decurrens**	
% of WS-10	Area (ha)	Seed.	Sapl.	Seed.	Sapl.	Seed.	Sapl.	Seed.	Sapl.	Seed.	Sapl.[1]
Tsuga heterophylla/ Castanopsis chrysophylla		426	241	190	113	31	26	103	82	5	5
39.2	4.02										
Tsuga heterophylla/ Rhododendron macrophyllum/ Gaultheria shallon		57	419	305	209	10	—	—	19	—	—
31.17	3.19										
Tsuga heterophylla/ Rhododendron macrophyllum/ Berberis nervosa		33	140	306	280	20	93	20	20	—	—
17.53	1.79										
Tsuga heterophylla/ Acer circinatum/ Polystichum munitum		33	33	217	283	50	17	—	—	33	—
12.09	1.24										

[1]Seed=seedlings < 1 m tall; sapl.=saplings > 1 m tall and < 15 cm dbh.

Tsuga heterophylla/Castanopsis chrysophylla associations **(Tshe/Cach)**

This community is the most widespread one on WS-10 (Table 3, Fig. 3). It is generally located on both north and south bounding ridges of WS-10. Westerly and southerly aspects are most common. The overstory tree stratum here is typically quite open relative to other forest types common to the area. Over 43 percent of the 0-cover class in WS-10 occurs in the *Tshe/Cach* habitat type. Most of the *Tshe/Cach* habitat type occurs beneath a very sparse primary tree canopy with 92.1 percent of the community having less than 50 percent cover in this layer.

The canopy of the understory tree stratum is very dense, reflecting the open overstory. Here 31.7 percent of the open understory tree stratum of WS-10 is in the *Tshe/Cach* habitat type. However, a much greater amount of the *Tshe/Cach* habitat type occurs with a denser understory tree cover.

The *Tshe/Cach* habitat type in WS-10 contains 1138 trees $\geq$ 15 cm dbh. Of these, 39 percent are *Castanopsis chrsophylla*, but only eight of them exceed 30 cm dbh. Thirty-three percent of the trees are *Pseudotsuga menziesii*; the species is well represented in the larger size class as well as reproductive classes. It is the dominant tree species and its abundance in the reproductive size classes insures its presence in late seral stages. *Tsuga heterophylla* is another common understory conifer.

A good indicator of the xeric nature of this habitat type is *Pinus lambertiana.* Eighty-two percent of the trees of this species occur within the *Tshe/Cach* habitat type of WS-

10. Some are over 120 cm dbh, although most are considerably smaller. Other less important trees in this habitat type include *Thuja plicata*, *Calocedrus decurrens*, *Acer macrophyllum*, *Taxus brevifolia*, *Cornus nuttallii*, and *Arbutus menziesii*.

Principal understory plant species and their cover values are shown in Table 3. The shrub stratum is dominated by *Rhododendron macrophyllum* followed in importance by *Acer circinatum* in the tall shrubs and *Gaultheria shallon* followed by *Berberis nervosa* in the low shrub layer. The herb layer is poorly developed and is dominated by *Xerophyllum tenax*. *Linnaea borealis* is also a common species. Moss cover is low, but 9 to 12 species are commonly present.

The *Tshe/Cach* habitat type is similar to both the *Psme-Tshe/Cococa* and the *Psme/*

TABLE 3. Percent cover of important plant species within Watershed 10 Habitat Types (from analytic plots) and the riparian zone (pers. comm., A. Campbell). (t=<0.5% cover measured; +=present in plots; M=mature; R=reprod.).

		Community Name				
Layer-Species		Tshe/Cach	Tshe/Rhma-Gash	Tshe/Rhma-Bene	Tshe/Accl/Pomu	Riparian
Tree Layer						
Pseudotsuga menziesii	M	18	20	22	11	+
	R	14	23	8	6	+
Tsuga heterophylla	M	15	16	25	43	+
	R	5	18	13	11	+
Thuja plicata	M	1	9	11	1	+
	R	t	—	3	2	+
Acer macrophyllum	M	—	4	4	20	+
	R	t	3	1	t	+
Pinus lambertiana	M	1	1	1	—	-
	R	4	2	1	—	-
Castanopsis crysophylla	M	40	1	2	—	-
Tall Shrub Layer						
Acer circinatum		13	30	29	19	+
Rhododendron macrophyllum		49	23	32	5	+
Cornus nuttallii		8	12	16	8	+
Castanopsis chrysophylla		13	1	1	t	+
Taxus brevifolia		1	7	8	10	+
Corylus cornuta		t	t	2	4	+
Low Shrub Layer						
Gaultheria shallon		45	25	18	3	+
Berberis nervosa		6	4	14	6	+
Herb Layer						
Xerophyllum tenax		13	1	1	t	-
Polystichum munitum		1	5	3	27	+
Linnaea borealis		4	4	4	1	+
Syntheris reniformis		t	1	1	1	+
Coptis laciniata		t	4	4	8	+
Viola sempervirens		t	1	t	t	+
Trillium ovatum		t	t	t	1	+
Vancouveria hexandra		t	t	t	1	+
Whipplea modesta		t	—	1	1	+
Oxalis oregana		—	—	t	1	+
Aralia californica		—	—	—	1	+
Adiantum pedatum		—	—	—	t	+
Blechnum spicant		—	—	—	t	+

Hodi habitat type of Dyrness *et al.* (1974) in its physiographic location, but the extreme development of the shrub layer distinguishes the *Tshe/Cach* habitat type.

Tsuga heterophylla/Rhododendron macrophyllum/Gaultheria shallon association **(Tshe/Rhme/Gash)**

This habitat type occupies only about 10 percent of WS-10 (Table 3, Fig. 3). It is typically patchy in distribution and located midway between ridgetops and major drainages. It is a more mesic habitat type than the *Tshe/Cach* habitat type (Zobel *et al.*, 1976).

The overstory tree stratum is commonly more dense than that of the *Tshe/Cach* habitat type. Again, the understory tree stratum is commonly denser than the overstory stratum with only 21.1 percent occurring with less than 25 percent cover. The habitat type contains an average of 292 trees larger than 15 cm dbh per ha. Of these, 45 percent are *Pseudotsuga menziesii*, which is found in nearly all size classes. The bimodal distribution of *Pseudotsuga menziesii* in this habitat type is similar to that found for WS-10 as a whole (Table 1). Tree density here is greater than in any other habitat type mapped.

The understory tree stratum is dense and composed of conifers and hardwoods. *Castanopsis chrysophylla* does not play as important a role in the total canopy cover in the *Tshe/Rhma/Gash* habitat type as it does in the *Tshe/Cach* habitat type. It is largely replaced by pole and sapling size classes of *Tsuga heterophylla.* Floristically, the *Tshe/Rhma-Gash* habitat type is similar to the *Tshe/Cach* habitat type. The moderately well developed tree layers do not prevent the development of a fairly dense tall and low shrub layer (Table 3). *Rhododendron macrophyllum* dominates the tall shrubs with *Acer circinatum* a common associate. *Gaultheria shallon* and *Berberis nervosa* dominate the low shrubs. The herb layer is poorly developed. *Linnaea borealis*, *Xerophyllum tenax*, *Chimaphila unbellata*, and *Polystichum munitum* are the most common species, but even these are found in small amounts.

Tsuga heterophylla/Rhododendron macrophyllum/Berberis nervosa association **(Tshe/Rhma/Bene)**

This habitat type occupies 8.71 percent of WS-10 (Table 3, Fig. 3). It is located primarily on northwest aspects, and occurs on a variety of slopes. It approximates the climatic climax habitat type at low to middle elevations (Dyrness *et al.*, 1974).

On WS-10 the *Tshe/Rhma/Bene* type has between 1 and 50 percent cover in the overstory tree canopy. However, the understory tree stratum is generally quite dense. The *Tshe/Rhma/Bene* habitat type contains 265 trees over 15 cm dbh per ha. Of these, 47 percent are *Tsuga heterophylla.* Most of the *Tsuga* is in small size classes. *Pseudotsuga menziesii* is the next most abundant tree and is the dominant tree as it makes up the total of larger size trees in this habitat type on WS-10. Smaller size classes of *Pseudotsuga menziesii* are also present.

The tall shrub stratum is generally less developed than in the more open *Tshe/Cach* and *Tshe/Rhma-Gash* habitat types. It is dominated by *Rhododendron macrophyllum* and *Acer circinatum. Vaccinium parvifolium* is also common. *Berberis nervosa* and *Gaultheria shallon* dominate a moderately developed low shrub layer. *Linnaea borealis* is the dominant herb (Table 3).

Tsuga heterophylla/Acer circinatum/Polystichum munitum associations **(Tshe/Acci/Pomu)**

This habitat type occupies 11.0 percent of WS-10 (Table 3, Fig. 3), almost all of which is adjacent to the drainage system in the lower portions of the watershed. Two small portions of WS-10, one on a bench and the other in a slight depression, have also been included in this habitat type although they probably more closely resemble a *Tsuga heterophylla/Polystichum munitum* habitat type (Dyrness *et al.*, 1974).

Cover in the overstory tree layer here is generally moderate. The *Tshe/Acci/Pomu* habitat type contains 258 trees over 15 cm dbh per ha in WS-10. Of these, 44 percent are *Tsuga heterophylla.* Again, most of the *Tsuga* are in small sizes. Dominance of *Pseudotsuga menziesii* in the overstory tree layer is still evident. There are, however, fewer large trees per ha in this habitat type.

The tall shrub layer is moderately well developed. *Acer circinatum*, the dominant, is patchy in distribution and low in stature. *Rhododendron macrophyllum*, an occasional associate, is also less robust than that found in other upland communities. The low shrub stratum is dominated by *Berberis nervosa.* The herb stratum is dominated by *Polystichum munitum*, and the moss layer shows greater development than in habitat types discussed above.

The mesic nature of the *Tshe/Acci/Pomu* habitat type is indicated by the dense herb cover and the high number of moist site indicator species such as *Polystichum munitum*, *Oxalis oregana*, *Vancouveria hexandra*, *Viola sempervirens*, and *Blechnum spicant* (Zobel *et al.*, 1976).

Pseudotsuga menziesii/Acer circinatum/Berberis nervosa community **(Psme/Acci/Bene)**

This community occupies 8.8 percent of WS-10 (Fig. 3). The *Psme/Acci/Bene* community occurs adjacent to the *Tshe/Rhma/Bene* community in almost all cases and represents a seral community within the *Tshe/Rhma/Bene* habitat type. The overstory tree layer of the *Psme/Acci/Bene* community is open and patchy in distribution. The overstory tree layer is similar to that in the *Tshe/Rhma/Bene* community in that it has a small percentage of the community occurring beneath cover classes 0 and 1. The *Psme/Acci/Bene* community in WS-10 contains an average of 257 trees larger than 15 cm dbh per ha. Here 45 percent are *Tsuga*, mostly of small size. There is also understory *Pseudotsuga menziesii*, evidence of the open nature of the community. The overstory tree stratum is dominated by scattered old-growth *Pseudotsuga menziesii* with only a few *Tsuga heterophylla* in the large size classes. *Tsuga heterophylla* dominates the understory tree stratum with *Thuja plicata* as a major associate in some areas.

The tall shrub stratum is dominated by *Acer circinatum. Rhododendron macrophyllum* is constant, but with low cover. Low shrubs are dominated by scattered *Berberis nervosa*, though *Gaultheria shallon* is also common. The herb stratum consists of a mixture of plants common to dry to mesic sites which indicate that the community may occupy slightly drier and warmer and more open sites than the climax *Tshe/Rhma/Bene* community. This fact explains in part why *Acer circinatum* dominates the typically less mesic seral stage of the *Tshe/Rhma/Bene* habitat type rather than *Rhododendron macrophyllum.*

Pseudotsuga menziesii/Acer circinatum/Gaultheria shallon community **(Psme/Acci/Gash)**

This community is the second most abundant plant community within WS-10 (Fig. 3).

It occurs on a variety of slopes and aspects. The *Psme/Acci/Gash* community normally occurs downslope of the *Tshe/Rhma/Gash* or *Tshe/Rhma/Bene* communities. Like the *Tshe/Cach* community, the *Psme/Acci/Gash* community has a sparse overstory tree layer cover. Over 81 percent of this community has less than a 25 percent overstory cover. The understory tree layer of the *Psme/Acci/Gash* community is patchy. The total open area in the overstory here is 30 percent of the cover class 0 of WS-10. The understory 0 cover class of this community accounts for 51.1 percent of that class on WS-10.

The *Psme/Acci/Gash* community contains 222 trees over 15 cm dbh per ha. *Tsuga heterophylla* and *Pseudotsuga menziesii* have nearly equal densities (38 percent and 36 percent of the total, respectively). *Pseudotsuga menziesii* dominates in total cover, however. Smaller size classes are well stocked with both *Pseudotsuga menziesii* and *Tsuga heterophylla.*

Acer circinatum dominates the tall shrub layer. This stratum may also contain small amounts of *Rhododendron macrophyllum. Gaultheria shallon* occurs with high cover values and dominates the low shrub layer, occasionally sharing dominance locally with *Berberis nervosa.* Mosses are moderately well developed in the more protected areas but occur with low cover values.

Riparian Community

The riparian community is the most limited of the seven communities in WS-10 (Fig. 3). It occurs mainly along the stream courses at low elevations and adjacent to the *Tshe/Acci/Pomu* community. The overstory and understory tree strata generally have between 25 and 50 percent cover, providing an open appearance. Stem maps show a marked increase in the number of logs on the ground surface within this and the adjacent *Tshe/Acci/Pomu* community compared to other plant communities on WS-10.

The overstory tree stratum of the riparian type is dominated by *Pseudotsuga menziesii* and *Tsuga heterophylla*, with local concentrations of *Acer macrophyllum*, *Thuja plicata*, and *Alnus rubra.* The understory tree stratum is dominated by *Tsuga heterophylla.*

The tall shrub stratum contains *Acer circinatum* and *Vaccinium parvifolium*; *Aralia californica* also occurs and is an indicator of the riparian environment. The sparse low shrub layer has scattered *Gaultheria shallon* and *Berberis nervosa.* The herb stratum is composed of a large number of moisture-loving genera.

Some small areas of less common communities are included in other major communities. One of these occurred often enough to warrant mention, the *Xerophyllum tenax* open (*Xete* open) type. The "*Xete* open" areas occupy 0.73 percent of WS-10, or nearly as much as the riparian community. It usually occurs on open slopes or ridgetops or near rock outcrops where soil development is limited. The *Xete* open type occurs most abundantly (91.1 percent of it) within the *Tshe/Cach* habitat type.

Habitat Types

The seven communities have been combined into four habitat types (HT) for stratification of the physical environment and vegetation during the modeling effort in WS-10. The habitat types are: (1) *Tshe/Cach* HT, consisting of the area occupied by the *Tshe/Cach* community; (2) *Tshe/Rhma/Gash* HT, consisting of the combined areas occupied by the *Tshe/Acci/Gash* and *Tshe/Rhma/Gash* communities; (3) *Tshe/Rhma/Bene* HT, an area occupied by the *Tshe/Rhma/Bene* and the *Psme/Acci/Bene* communities;

and (4) the *Tshe/Acci/Pomu* HT, which combines the areas occupied by the *Tshe/Acci/Pomu* and riparian communities (Fig. 3).

The communities and habitat types represented in WS-10 are similar to stands representative of their respective types on other portions of the H. J. Andrews Experimental Forest and other western Cascade sites in Central Oregon (Franklin *et al.*, 1970; Franklin and Dyrness, 1973; Dyrness *et al.*, 1974; Franklin *et al.*, 1972).

Summary

Watershed 10 is a mosaic of mature and old-growth stands dominated by *Pseudotsuga menziesii*. Communities are those common to low elevations in the *Tsuga heterophylla* Zone. They span most of the range or gradient in temperature and moisture for this zone.

Seven communities were identified and mapped during this study: *Tshe/Cach*, *Tshe/Rhma/Gash*, *Tshe/Rhma/Bene*, *Tshe/Acci/Pomu*, *Psme/Acci/Gash*, and *Psme/Acci/Bene* communities and the riparian vegetation type. These communities are representative of four major habitat types.

Intensive stem and vegetation mapping has yielded numerous data on the structure and composition of plant communities. These data provide a sound base for environmentally and biologically stratifying the watershed for ecosystem modeling projects.

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Factors Affecting Nitrogen and Phosphorus Levels in Canyon Ferry Reservoir, Montana, and Its Effluent Waters[2]

Abstract

A two-year limnological investigation was performed to determine the trophic status of Canyon Ferry Reservoir, Montana: it revealed some interesting phenomena, with particular regard to nitrogen. Throughout the study there was always more inorganic nitrogen in the outflow compared to the inflow. This finding appeared to be due to large populations of the heterocystus blue-green alga *Aphanizomenon flos-aquae*. The extent of spring drawdown was probably influential in regulating the quantity of inorganic nitrogen regenerated within the reservoir each year. This factor in turn affected the relative abundance of the ensuing phytoplankton taxa. There was considerable mineralization of combined phosphorus after it entered the reservoir; however, there was essentially no difference between influent and effluent total phosphorus loads.

Introduction

A limnological study was performed during 1971-1973 on Canyon Ferry Reservoir, the Missouri River, and its headwater streams to document any changes which had occurred in the reservoir since its impoundment (Rada, 1974). In addition to elucidating the basic limnological character of the reservoir, this study revealed some interesting features regarding the possible effects of reservoir design and management on nitrogen and phosphorus cycles.

Description of the Study Area

Canyon Ferry Reservoir is an impoundment (Canyon Ferry Dam) of the Missouri River approximately 24 km east of Helena, Montana. The reservoir, which initially reached maximum pool elevation during the summer of 1955, is used for power production, flood control, irrigation, recreation, and a supplemental water supply for the city of Helena. The Missouri River is formed by the confluence of the Gallatin, Madison, and Jefferson rivers approximately 80 km upstream from Canyon Ferry Dam. The drainage area has a range of land uses including agriculture, grazing, timbering, and recreation. At the dam the Missouri River has a total drainage area of 41,192 km^2. Morphometric data for the reservoir at maximum pool elevation (1158 m above mean sea level) are shown in Table 1. A generalized map of the study area is presented in Figure 1.

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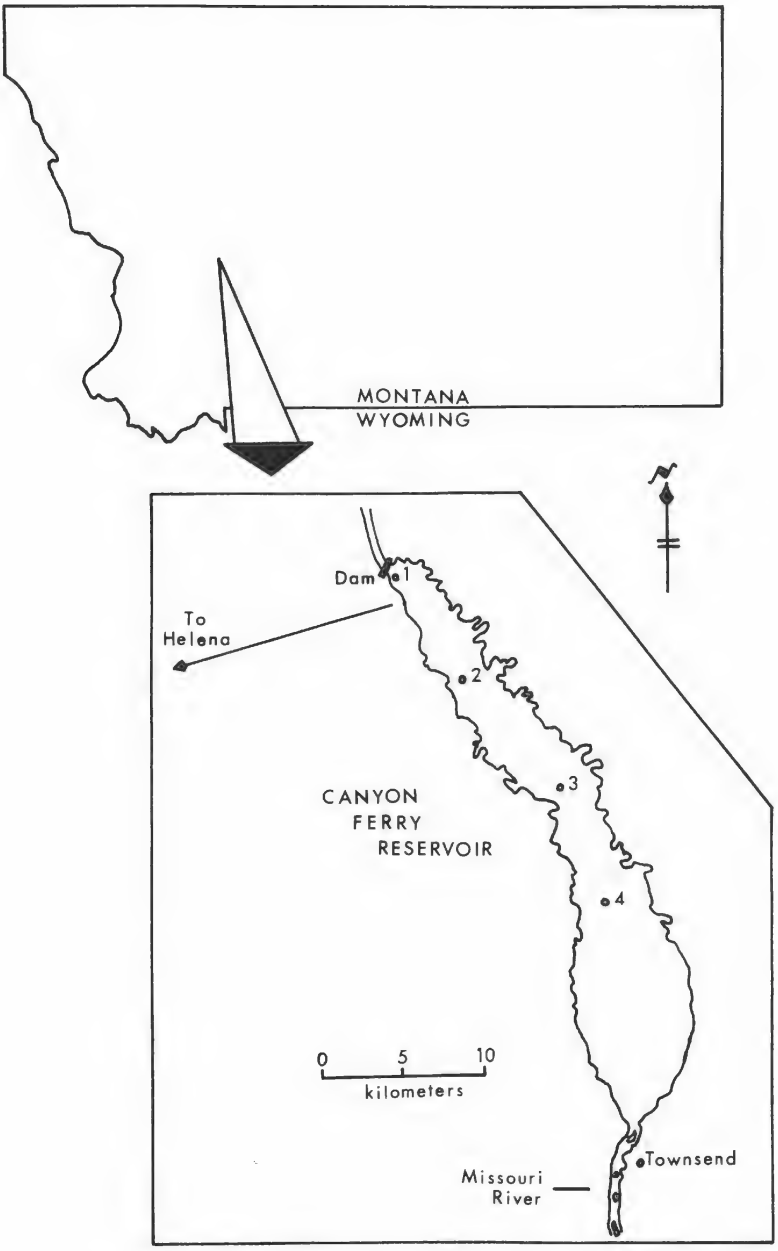

Figure 1. A map of the study area. The locations of the sampling stations within the reservoir are indicated by numbers 1-4.

TABLE 1. Morphometric and hydrologic data for Canyon Ferry Reservoir.

Maximum depth	50.1 m (164.4 ft)
Mean depth	17.8 m (58.3 ft)
Discharge depth	27.0 m (88.6 ft)
Maximum length	40.2 km (25 mi)
Maximum breadth	7.2 km (4.5 mi)
Mean breadth	3.5 km (2.2 mi)
Maximum surface area	14,238 ha (35,181 acres)
Maximum volume	2,530 x 10^6 m^3 (2,050,900 acre-ft)
Mean annual discharge	6,016 x 10^6 m^3 (4,876,704 acre-ft)
Length of shoreline	122.3 km (76 mi)
Shoreline development	2.89
Slope of basin	0,12%

Methods and Materials

Water samples were collected at weekly intervals from mid-May to mid-September of 1971 and 1972 and at monthly intervals from mid-September 1972 through late April 1973.

Four stations were located in the reservoir, one near the dam and three at approximately 8 km (5 mi) intervals upstream (Fig. 1). Stations were also located in the Missouri River at Townsend (inflow) and directly downstream from the dam (outflow). Data presented for the reservoir are averages from all reservoir stations.

Water samples were taken with a 3-l Van Dorn bottle at 5-m intervals from the surface to the bottom of the reservoir at each station. In addition, euphotic zone composite samples were made from water taken at 1-m intervals through the euphotic zone.

The reduction method of Mullen and Riley (Barnes, 1959) was used in the analysis of nitrate, and that of the APHA (1971) for nitrite. Ammonia was determined with the phenolhypochlorite method of Solorzano (1969). The sum of nitrate, nitrite, and ammonia is expressed as total inorganic N. Total phosphate and dissolved orthophosphate were estimated by the single reagent method (EPA, 1971). Combined phosphate was computed as the difference between total phosphate and dissolved orthophosphate.

Phytoplankton standing crop was determined for each euphotic zone composite sample according to the membrane filter concentration technique (APHA, 1971).

Hydrologic data were supplied by the United States Geological Survey (1971 and 1972) and the United States Bureau of Reclamation (unpublished data).

Results and Discussion

Canyon Ferry Reservoir was determined to be primarily a calcium bicarbonate water. Its phytoplankton flora, more than sixty species, was composed primarily of blue-green algae and diatoms. *Aphanizomenon flos-aquae* was the most abundant species, while *Fragilaria crotonensis*, *Stephanodiscus niagarae*, *Melosira granulata*, and *Diatoma elongatum* were also prominent. *Daphnia schodleri* was the most abundant zooplankter; however, *Cyclops bicuspidatus thomasi* was also prevalent early in the season (Martin, 1975). Previously Canyon Ferry had been found to be highly productive (Wright, 1959; 1961; 1965), but by 1971-1972 it appeared to be approaching a lower steady-state level of biological production (Martin, 1975; Rada, 1974). At the time of this study, it could be classified as moderately productive or slightly eutrophic.

The N-loading data are presented in Table 2. During the summer of 1971, the net outflow of nitrate was nearly twice that of the inflow. The same phenomenon occurred

during the summer of 1972 as well as during the 12-month period between May 1972 and April 1973. Ammonia and nitrite also behaved in a similar manner; however, nitrite never contributed more than 3.5 percent of the total inorganic nitrogen loads. Since the majority of the water discharged from the reservoir was withdrawn from a depth greater than 25 m, it is not unusual that large nitrogen loads were discharged. However, this fact does not explain the continuously greater outflow of inorganic nitrogen as compared to the inflow.

TABLE 2. A comparison of the inorganic nitrogen and orthophosphorus loads (kg N and P) for the inflow and outflow of Canyon Ferry Reservoir.

Data	Location	NO_2 + NO_3 -N	NH_3-N	Total Combined Inorganic-N	Ortho-P
15 May 1971	Inflow	154,550	84,010	238,560	60,464
to	Outflow	303,084	97,038	400,122	88,492
18 Sept. 1971	Difference	+148,534	+13,028	+161,562	+28,028
13 May 1972	Inflow	110,225	77,553	187,778	82,992
to	Outflow	191,655	82,992	274,647	80,820
18 Sept. 1972	Difference	+81,430	+5,439	+86,869	-2,127
13 May 1972	Inflow	379,985	96,003	475,988	163,169
to	Outflow	583,308	130,186	712,494	216,968
26 Apr. 1973	Difference	+202,323	+34,183	+236,506	+53,799

Euphotic zone concentrations of inorganic nitrogen decreased and remained low during July and August of each year (Figs. 2 and 3). In fact, nitrate was often undetectable at various stations during these periods. The increase in diatom standing crop during July 1971, when the combined inorganic nitrogen concentration was low, could be due to an internal storage of nitrogen within the cells earlier in the season when nitrogen was more abundant. The bloom of blue-green algae which occurred when nitrogen was low is most easily explained by N_2-fixation. *Aphanizomenon flos-aquae*, which was by far the most abundant alga in Canyon Ferry, is now considered to be an important fixer of elemental nitrogen in aquatic ecosystems (Brezonik, 1972; Horne and Goldman, 1972; Stewart, 1968; Vanderhoef *et al.*, 1974). Vanderhoef *et al.* (1974) also showed in parts of Green Bay that as the inorganic nitrogen concentrations decreased, *Aphanizomenon* increased in standing crop relative to algae not capable of N_2-fixation. They further showed that as inorganic nitrogen continued to decrease, the N_2-fixation efficiency of *Aphanizomenon* increased. High rates of N_2-fixation have significantly contributed to the nitrogen budgets of other lakes; e.g., Clear Lake (Horne and Goldman, 1972), areas of Green Bay (Vanderhoef *et al.*, 1974), and Lake Erken (Granhall and Lundgren, 1971).

The inorganic nitrogen data for Canyon Ferry show an internal loading of 16.6 kg ha^{-1} yr^{-1}. This figure indicates that approximately one-third of the inorganic nitrogen in the outflow appears to be derived from internal sources. Accordingly, it seems highly probable that nitrogen fixation was a significant source of internal nitrogen loading in the reservoir and aids in the explanation as to the continuously larger outflow of inorganic nitrogen as compared to the inflow.

Recycling a substantial portion of the fixed nitrogen would have been delayed until the algal cells had decomposed and mineralization had occurred. Much of this process would have taken place in the deep water and sediments. Furthermore, exposing sedi-

ments to the air during drawdown may contribute to the nitrogen supply of water by accelerating decomposition (Toetz, 1973). Consequently, the hydrologic regime of Canyon Ferry Reservoir could have significantly affected the amount of nitrogen recycled each year. Possible evidence to support the latter comes from the observation that during spring drawdown in 1972 the area of reservoir bottom exposed to the atmosphere was approximately 71 percent of that exposed during 1971 (3913 ha); correspondingly, the discharge of inorganic combined nitrogen during the summer of 1972 was approximately 69 percent of that discharged in 1971 (Table 2).

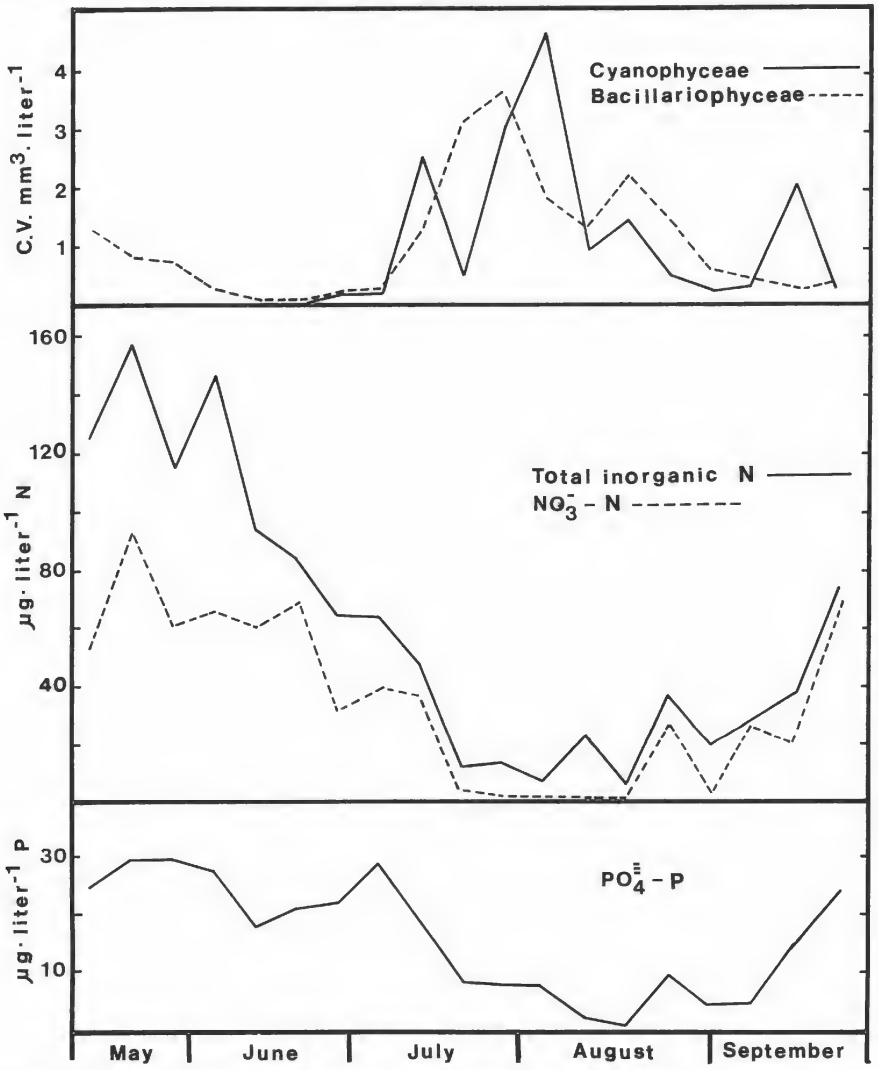

Figure 2. Seasonal euphotic zone concentrations of total inorganic nitrogen, nitrate, and orthophosphorus together with mean bacillariophycean and cyanophycean standing crops during 1971.

When data for the period of May 1972 through April 1973 are considered, the average discharge of regenerated nitrogen was 19,709 kg N per month. This figure compares with an average of 31,053 kg N per month being released and discharged during the summers of 1971 and 1972; i.e., when the previously exposed sediments were being flooded. Hence, regeneration of inorganic nitrogen occurred to a greater extent during the period following drawdown than during the remainder of the year.

The euphotic zone concentration of inorganic nitrogen was also substantially lower during the summer of 1972 as compared to 1971, the year of greater spring drawdown

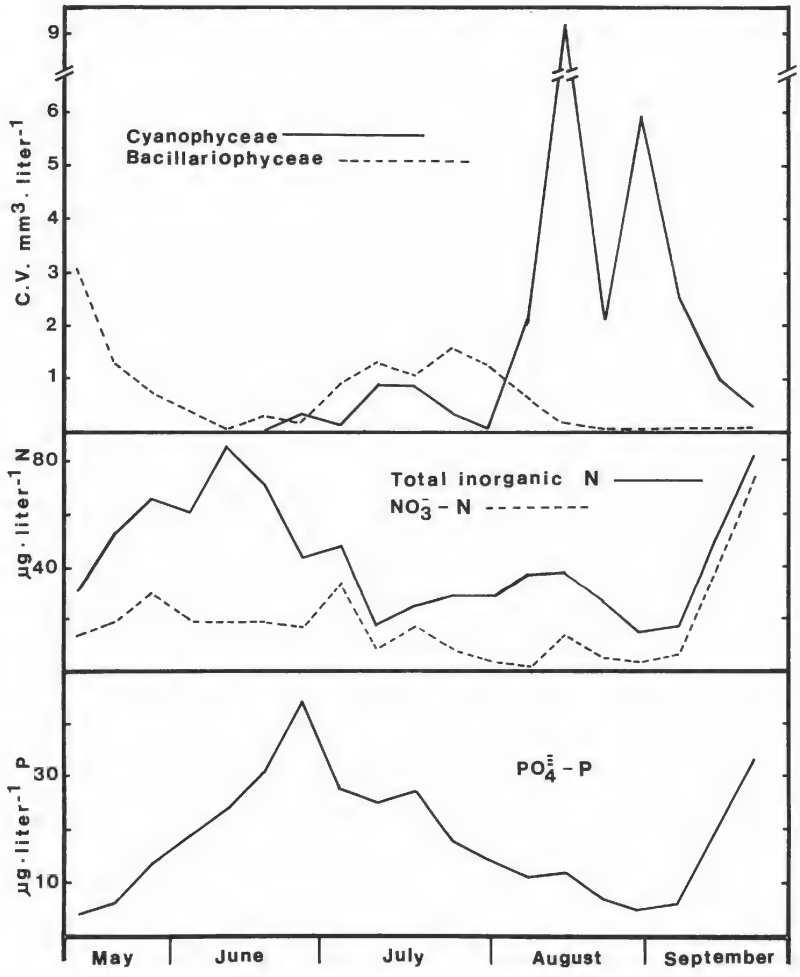

Figure 3. Seasonal euphotic zone concentrations of total inorganic nitrogen, nitrate, and orthophosphorus together with the mean bacillariophycean and cyanophycean standing crops during 1972.

(Figs. 2 and 3). This change seemed to have a notable effect on the seasonal abundance of phytoplankton. During 1971 more nitrogen was available for assimilation and diatoms were more abundant. Conversely, less nitrogen was available in 1972 and the diatom standing crop did not approach its density of 1971. During 1972, however, the blue-greens surpassed their 1971 maximum and average standing crop. These results are consistent with the idea that the diatoms may have been ultimately nitrogen-limited, whereas the blue-greens could still flourish due to their ability to fix molecular nitrogen. These data indicate that the relative seasonal abundance of the phytoplankton taxa was influenced at least in part by management of spring drawdown which significantly affected the amount of nitrogen recycled each year.

The highest concentrations of both total and orthophosphorus in the influent waters occurred during June of each year and were associated with peak runoff and high turbidities (Rada, 1974). A similar relationship between phosphorus and turbidity was also shown by Soltero *et al.* (1973) for the Big Horn and Shoshone rivers of Wyoming.

More dissolved orthophosphate was observed in the outflow than inflow during each summer as well as during the period of May 1972 through April 1973 (Table 2). There was, however, no net change in the total phosphate within the reservoir when the total phosphate budget was determined for the period of June 1972 through April 1973 (Table 3). This finding would indicate that even though Canyon Ferry had a high areal loading of phosphate (2.15 g total-P m^{-2} during June 1972 through April 1972 and 1.27 g ortho-P m^{-2} during May 1972 through April 1973), there was very little retention of phosphorus within the reservoir. The tables also indicate that much of the combined phosphate entering the reservoir was mineralized to dissolved orthophosphate and discharged via the deep-water withdrawal. Much of the phosphorus entering Canyon Ferry was therefore never available for biological assimilation in the euphotic zone.

TABLE 3. A comparison of the phosphorus loads (kg P) for the inflow and outflow of Canyon Ferry Reservoir.

Dates	Location	Total-P	Combined-P	Ortho-P
12 June 1972—	Inflow	276,147	160,473	115,674
	Outflow	277,349	73,118	204,231
26 April 1973	Difference	+1,202	-87,355	+88,557

Summary and Conclusion

Approximately one-third (16.6 kg ha^{-1} yr^{-1}) of the inorganic combined nitrogen observed in the outflow of Canyon Ferry resulted from internal loading; i.e., N_2-fixation and sediment release/mineralization of nitrogen. We attribute this phenomenon to the presence of large *Aphanizomenon* standing crops which could have potentially fixed N_2 during the summer when the demand for inorganic nitrogen was greater than the supply. The data also indicate that the amount of nitrogen released from the sediments to the reservoir was related to the extent of drawdown. With the rise in water level following drawdown, the soluble nitrogen compounds resulting from organic decomposition were released to the reservoir. Consequently, more nitrogen was available for assimilation by phytoplankton following more extensive drawdown. These conditions favored relatively large, persistent populations of diatoms. Blue-greens, on the other hand, established relatively larger standing crops than other phytoplankton taxa when the preceding spring drawdown was less extensive.

The limnological characteristics of Canyon Ferry demonstrate the significance of reservoir design and management on the water quality within the reservoir as well as downstream. It appears that the hydrologic regime and nitrogen fixation significantly affected its nitrogen budget as well as the relative seasonal abundance of the phytoplankton taxa. The absolute quantity of nitrogen contributed by *Aphanizomenon* will, however, require actual measurements of N_2-fixation rates within the reservoir. More extensive investigations on the effects of drawdown on nitrogen cycling are also needed.

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Estimation of Fat from Femur Marrow of Oregon Black-Tailed Deer[1]

Abstract

Femur marrow samples from 27 Oregon black-tailed deer (*Odocoileus hemionus columbianus*) were analyzed for percentage content of fat, water, and residue. Percentage of fat was significantly inversely correlated to percentage of water (r^2=0.98, d.f.=25). Evidently an accurate measure of fat content can be extrapolated by accurately measuring water content.

Measurement of fat concentration in the femur marrow of an ungulate can indicate the state of the animal's energy reserves. Ether extraction of fat by traditional methodology is time consuming, and other, less accurate methods of deducing fat content of marrow have been devised (Cheatum, 1949; Greer, 1968). Verme and Holland (1973) developed a rapid reagent-dry assay method, but estimates of femur fat concentrations derived from their rapid method and the more laborious ether extraction methods were dissimilar.

Bischoff (1954) indicated that most of the dry weight of femur marrow from both mule deer (*O. h. hemionus*) and black-tailed deer was fat. Neiland (1970) demonstrated that the weight of dried femur marrow in caribou (*Rangifer tarandus*) was nearly equal to the weight of the fat in the marrow. He postulated that the marrow in deer and caribou was essentially a three-component system comprised principally of water and fat, and that as fat is deposited within the marrow, water is driven off. Likewise, as fat is used during nutritionally stressful periods, resulting space in the marrow is filled by water, presumably because replacement by water would have the lowest metabolic cost to the animal.

This study was designed to determine whether the relationship between amounts of water and fat in femur marrows of black-tailed deer was sufficiently precise to enable prediction of fat content from accurate measurements of water content. Deer were collected with permission of the Oregon Department of Fish and Wildlife. K. R. Hall and T. P. Kistner aided in collection of deer, and J. Early aided in laboratory analyses.

Methods

Femurs were obtained from the carcasses of 27 black-tailed deer (4 fawns, 8 yearlings, 15 adults) collected by shooting between 31 August 1976 and 23 February 1977 and frozen until analysis. Deer were collected from three distinct areas: 1) The Alsea Ranger District, Siuslaw National Forest, in the Coast Range (n=13); 2) The William L. Finley National Wildlife Refuge in the Willamette Valley (n=9); and 3) The Willamette National Forest in the Oregon Cascades (n=5).

[1]Oregon State University, Agricultural Experiment Station Technical Report No. 4601.

The approximate center third of each femur was cut out with a lapidary saw, and the marrow removed. Marrow samples were weighed to the nearest hundredth of a gram, and dried in a forced-air drying oven at 60°C for 2-3 days, or until weight loss ceased. The samples were then weighed to extrapolate water loss. Each sample was then placed in a soxhlet extraction thimble and the fat extracted with a 2:1 solution of chloroform and methanol (Bloor's reagent) for 24 hours. The remaining residue was weighed after drying, and the amount of extracted fat was calculated.

Results and Discussion

Fat concentration ranged from 12 to 92 percent, and water concentration from 7 to 74 percent (Figure 1). Percentage of fat was significantly inversely correlated to percentage of water ($r=0.99$, $P<0.01$, d.f.=25).

Amount of residue ranged from 1 to 20 percent, and was significantly inversely correlated to percentage of fat ($r=0.86$, $P<0.01$, d.f.=25). Although Neiland (1970) found a similar relationship in caribou femurs, caribou appear to have a considerably

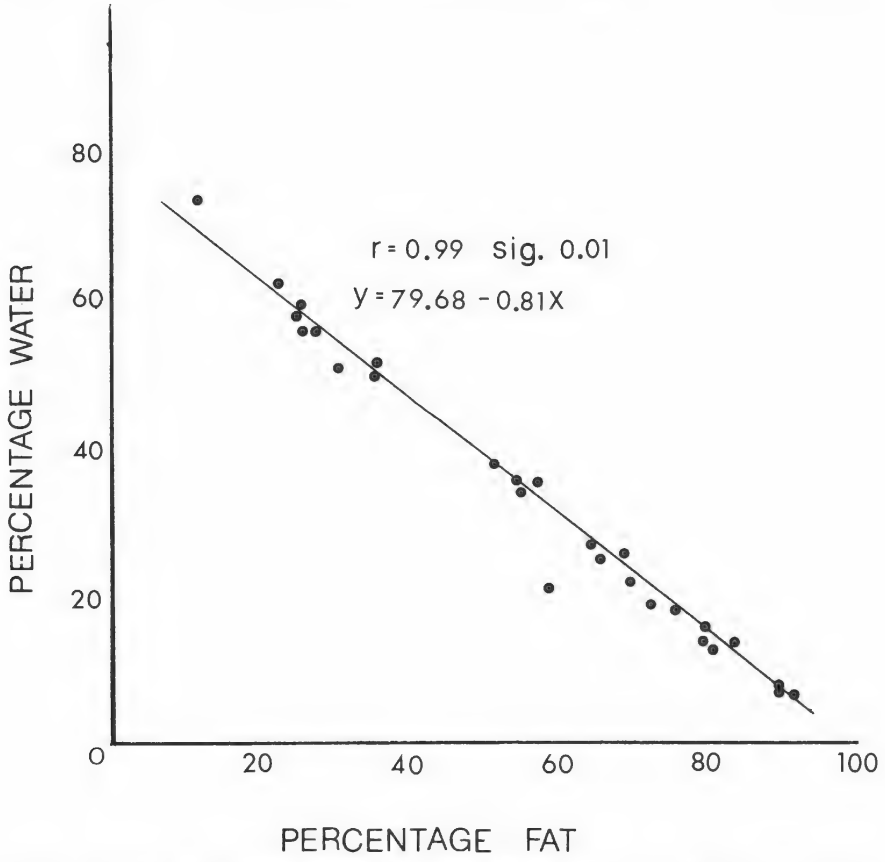

Figure 1. Relationship between percentage fat and percentage water in femur marrows from Oregon black-tailed deer.

narrower range of residue content (2-6 percent vs. 1-20 percent) than black-tailed deer.

The strong relationship between fat and water concentration indicated that for black-tailed deer, an accurate prediction of concentration of fat content in the femur could be made by accurately measuring water content. This hypothesis was suggested by Verme and Holland (1973), who worked with estimation of femur marrow fat in white-tailed deer (*O. virginianus*). For their estimations they assumed that the white-tails had a similar range of residue in the marrow as did caribou. If white-tails are at all similar to the black-tails examined in this study, however, their assumption may be incorrect. In fact, Verme and Holland (1973) obtained higher values for fat concentration with their reagent-dry method than with ether extraction, and proposed among other possibilities that white-tailed deer marrow might contain proportionately more residue than was found in caribou.

If the relationship between percentage of fat and percentage of water is as highly correlated for other ungulates as it is for Oregon black-tails, only a small number of femurs would be required to predict fat content accurately in the marrow by measuring water content of the marrow.

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Parasitic Mites of Voles of the Genera Arborimus and Lagurus in Oregon[2]

Abstract

During studies of Oregon mammals, 33 individuals of the white-footed vole (*Arborimus {=Phenacomys} albipes*), 17 individuals of the red tree vole (*A. longicaudus*), and 98 individuals of the sage vole (*Lagurus curtatus*) were examined for ectoparasitic mites.

Introduction

Relatively little information on parasitic mites from these species is available (Whitaker and Wilson, 1974). The purpose of this paper, therefore, is to present data on ectoparasites that we have collected from 1969 through 1977.

Methods and Materials

Mites were collected by brushing the voles' fur with a finely bristled toothbrush. Voles were then examined with the aid of a 16-power handlens and by blowing the fur. Mites that had been missed were picked off using a forceps.

Mites were preserved in 70 percent ethanol. They were cleared and stained in Nesbitts solution containing acid fuchsin, and mounted on slides in Hoyer's solution.

Study Area and Habitat

White-footed voles and red tree voles occupy the Coast Ranges, Klamath Mountains, and Western Cascades physiographic provinces of western Oregon (Franklin and Dyrness, 1973). Within these provinces, the voles inhabit the Sitka Spruce (*Picea sitchensis*) and Western Hemlock (*Tsuga heterophylla*) Zones of Franklin and Dyrness (1973). Their primary habitats are: (1) white-footed vole—Riparian Alder/Small Stream (Maser and Franklin, 1974; Maser and Johnson, 1967); and (2) red tree vole—Mature and Immature Conifer (Douglas-fir variant) (Maser, 1966; Maser and Franklin, 1974).

Sage voles inhabit the Columbia Basin, High Lava Plains, Basin and Range, and

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Owyhee Upland physiographic provinces of central and Eastern Oregon (Franklin and Dyrness, 1973). Within these provinces, sage voles are known to occupy the Pumice Region, Steppe (with bunchgrass), Shrub-steppe (with big sagebrush, *Artemisia tridentata*), the Alpine Region of Steens Mountain, and the Western Juniper (*Juniperus occidentalis*) Zone (Franklin and Dyrness, 1973; Maser *et al.*, 1974; Maser and Strickler, 1978).

Results and Discussion

Arborimus longicaudus. Of the 17 red tree voles examined, 15 harbored mites (Table 1). The more abundant mites were *Androlaelaps fahrenholzi* and *Glycyphagus* (=*Dermacarus*) *hypudaei. Androlaelaps fahrenholzi* is a widespread laelapid mite found on many different species of wild mammals (Whitaker and Wilson, 1974). *Glycyphagus hypudaei* is a non-feeding hypopial (transport stage) mite likewise occurring on many species of mammals. Two individuals of a new species of myobiid mite, *Radfordia arborimus* (Fain and Whitaker, 1975), were found along with a new genus and species of Listrophorid which is still under study.

Arborimus albipes. Thirty-three white-footed voles were examined—all but one harbored mites (Table 1). Mites taken in greatest numbers on this species were again *A. fahrenholzi* and *G. hypudae. Haemogamasus ambulans* also occurred on these voles, as did the same listrophorid species found on red tree voles. In addition, several species of the non-parasitic genus *Euryparasitus* were collected.

Lagurus curtatus. Of 98 sage voles examined, 42 were found to harbor mites (Table 1). Again, the most abundant mite was *A. fahrenholzi.* This species was found on 38 animals, or 38.8 percent of the total sample, and 90.4 percent of those with mites. The mite averaged 3.92 individuals per animal, and 10.1 per animal on those harboring this species. The only other rather abundant mite was the same hypopus, *G. hypudaei,* found on the two species of *Arborimus.* Several other species of mites were taken, however, including 20 individuals of a second hypopus, which were similar to *Dermacarus hylandi.* Unfortunately, they were poorly preserved and could not be positively identified.

At least one new species of mite, *Radfordia arborimus* (Fain and Whitaker, 1974), was identified from the red tree vole during this study and *Listrophorus mexicanus* represents a new record from Oregon. Only *Haemogamasus reidi* had been previously reported from the white-footed vole, and only *A. fahrenholzi* on the red tree vole; the rest of the parasitic forms are new host records (Whitaker and Wilson, 1974). *Hirstionyssus utahensis*, *G. hypudaei*, *D. hylandi*, and *Listrophorus mexicanus* had not been previously taken from the sage vole.

Conclusion

Red tree voles, white-footed voles, and sage voles have a common denominator that probably accounts for heavy mite infestations; namely, these voles spend much time in their nests. Although red tree voles are arboreal, their nests often are large and compact and usually are moist, simulating subterranean habitat. Both the white-footed vole and the sage vole are terrestrial and subterranean in nesting habits (Maser, 1966; Maser and Franklin, 1974; Maser and Johnson, 1967; Maser *et al.*, 1974). Thus, the microenvironment of nests appears to be a major factor in the development and maintenance of large complements of mites.

TABLE 1. Ectoparasitic and other associated mites of the fur of **Arborimus albipes**, **A. longicaudus**, and **Lagurus curtatus** from Oregon.

	Arborimus albipes				**A. longicaudus**				**Lagurus curtatus**			
	Infested		**No. mites**		**Infested**		**No. mites**		**Infested**		**No. mites**	
	No.	%	Total	$\bar{x}$	No.	%	Total	$\bar{x}$	No.	%	Total	$\bar{x}$
No. examined	33				17				98			
					Parasitic or Phoretic Forms							
Laelapidae												
Androlaelaps fahrenholzi	27	81.8	513	15.55	15	88.2	492	28.9	38	38.8	384	3.92
Eulaelaps stabularis	3	9.1	3	0.09	—	—	—	—	—	—	—	—
Haemogamasus ambulans	5	15.2	25	0.76	—	—	—	—	—	—	—	—
H. occidentalis	1	3.0	1	0.03	—	—	—	—	—	—	—	—
H. reidi	—	—	—	—	—	—	—	—	4	4.1	6	0.06
Hirstionyssus isabellinus	—	—	—	—	—	—	—	—	4	4.1	8	0.08
H. utahensis	—	—	—	—	—	—	—	—	2	2.0	2	0.02
Glycyphagidae												
Glycyphagus hypudaei	5	15.2	24	0.73	8	47.1	182	10.7	15	15.3	123	1.26
Dermacarus hylandi (possibly—specimens in poor shape)					—	—	—	—	1	1.0	20	0.20
Listrophoridae												
Listrophorid gen. & sp. nov.	1	3.0	20	0.61	1	5.9	100	5.9	—	—	—	—
Listrophorus mexicanus	—	—	—	—	—	—	—	—	1	1.0	2	0.02
Myobiidae												
Radfordia arborimus	—	—	—	—	2	11.8	2	0.12	—	—	—	—
					Other Associates							
Cyrtolaelapidae												
Euryparasitus sp.	11	33.3	28	0.85	—	—	—	—	3	3.1	3	0.03
Anoetidae sp.	—	—	—	—	3	17.6	5	0.29	—	—	—	—
Ascidae												
Proctolaelaps sp.	—	—	—	—	—	—	—	—	3	3.1	5	0.05
Ameroseiidae												
Kleemania sp.	—	—	—	—	—	—	—	—	1	1.0	1	0.01

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Western Extent of the Shuksan and Church Mountain Thrust Plates in Whatcom, Skagit, and Snohomish Counties, Washington

Abstract

The westward-yielding Shuksan and Church Mountain thrusts of mid-Cretaceous age can be traced throughout the western foothills belt of the North Cascades. Phyllites of the Shuksan Thrust Plate extend as far west as Samish Bay and Samish Island. Although not everywhere present, an imbricate zone below the phyllites of the Shuksan Thrust Plate is characterized by slices of metaplutonic rocks, including probable Yellow Aster Complex, intermixed with greenstones, metasedimentary rocks, ultramafic rocks, and locally with phyllites of the Shuksan Suite. The imbricate zone is exposed south of the Skagit Valley in the Table-Haystack Mountain area; in isolated outcrops in the lower Skagit Valley; and in several windows and half-windows along the shore of Samish Bay at the southern end of Chuckanut Drive, and on Chuckanut Mountain.

Discontinuous zones of imbrication and/or faulting within the Shuksan Thrust Plate include slices of metavolcanic rocks and slices of crystalline rocks associated with ultramafic rock.

Rocks ascribed to the Church Mountain Thrust Plate and associated imbricate zone can be traced eastward from the Devils Mountain area near Mount Vernon toward Lake Cavanaugh. Windows exposing the Mesozoic "autochthon" below the Church Mountain Thrust are along the axis of an Eocene anticline that trends northwesterly from Lake Cavanaugh toward Sedro Woolley and Chuckanut Mountain. Windows and half-windows through the overriding Shuksan Thrust Plate also occur along this anticlinal trend.

The thrust plates are terminated on the south by the Late Tertiary Devils Mountain fault.

Introduction

The area under investigation, as outlined on Figure 1, is part of the low western foothills of the Cascades; elevations range from sea level to over 1300 m (4000 ft). The primary purpose of this study was to determine the western extent of the mid-Cretaceous thrusts (Misch, 1960) which have been traced throughout the western flank of the North Cascades by Misch (1952-1977), Vance (1957), Jones (1959), and Ragan (1963). Most of the foothill belt described in this report was mapped in reconnaissance by Miller while in the employ of Union Oil Company of California (Miller, 1961). Part of the findings of that work were reported by Miller (1969), Miller and Misch (1963), and Misch (1966, 1977).

Summary of Regional Setting

The geologic history of the North Cascades can be traced back to Precambrian times. Precambrian and Early Paleozoic crystalline basement (Misch, 1960, 1966, 1976; Mattinson, 1972; for the San Juan Islands, Danner, 1967, 1968, 1977; and Vance, 1975, 1977) may underlie this entire region, to judge from the numerous Yellow Aster slivers along the Shuksan Thrust on the east; by the Turtleneck Complex on Orcas Island on the west; and by the intervening autochthonous fault slice of Yellow Aster on Vedder Mountain (Misch, 1966, 1977).

Misch (1976) summarizes the geosynclinal setting of this region as follows: "A

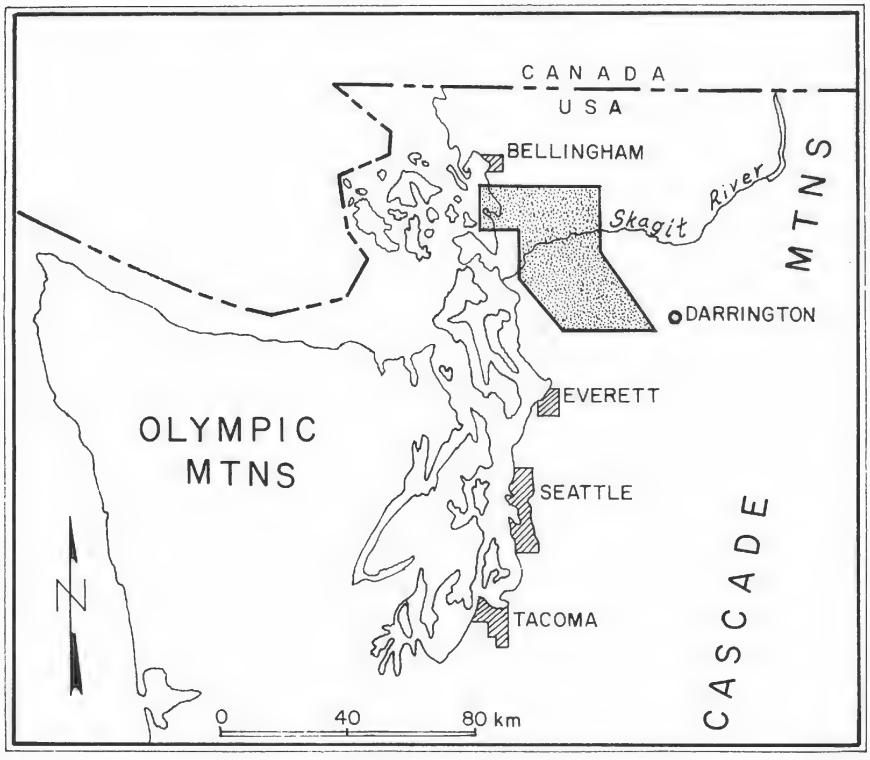

Figure 1. Index map showing location of area discussed in this report.

basement of predominantly quartz-dioritic composition contains the record of Precambrian and Caledonian plutonic and metamorphic events. Devonian to Cretaceous intermittent deposition of sedimentary and volcanic rocks of eugeosynclinal character was endosialic and occurred in tectonic settings of island arc affinity."

The geosynclinal phase was terminated by an intense mid-Cretaceous orogeny which produced the two large west-yielding Shuksan and Church Mountain Thrusts (Misch, 1960) on the western flank of the range. The upper unit of this thrust system (Shuksan Plate) has been traced for 150 km along strike (Misch, 1966, including data from Vance, 1957; and Yeats, 1964), whereas the southern continuation of the Church Mountain Plate beyond the Skagit region remains in doubt. North of the Skagit, the system has a combined westward relative displacement of at least 125 km. The present report discusses the geology along the frontal portion of the two thrust sheets in Whatcom, Skagit, and part of Snohomish Counties.

Subsequent to post-orogenic continental deposition on the partially eroded thrust sheets, a moderate to strong Early or Middle Eocene orogeny produced predominantly northwest trends. Late Eocene (?) to Miocene clastic deposition in the western part of the foothill belt was followed by mild folding and faulting of probable Miocene and younger age.

Pre-late Cretaceous Stratigraphic-Structural Units

Three major stratigraphic-structural units that predate the Late Cretaceous and Cenozoic strata are (1) the Shuksan Thrust Plate composed of presumably pre-Jurassic metamorphic rocks; (2) the Church Mountain Thrust Plate consisting of Paleozoic and minor Mesozoic rocks; and (3) the Autochthon of Mesozoic and Paleozoic strata. The term "Autochthon" as used here does not preclude the possibility of unrecognized major thrusting in this unit (see also Misch, 1977).

Shuksan Thrust Plate and Associated Rocks

Included in this unit, as mapped in this report, are the Shuksan Metamorphic Suite (Darrington Phyllite, Shuksan Greenschist) of the thrust plate, and associate slices of crystalline rocks including presumed Yellow Aster Complex, ultramafic rocks, and certain meta-sedimentary and volcanic rocks which occur in an imbricate zone near the sole of the thrust. All of the above rock units as well as the imbricate zone were named and described by Misch (1960, 1966).

Shuksan Metamorphic Suite

As described by Misch (1966, p. 109), "The lower unit (Darrington Phyllite) consists of pelitic and semipelitic, commonly quartz-rich phyllites which in some areas grade into schistose feldspathic metagrawackes." For the most part, the phyllites are dark gray to black containing thin layers of quartz $\pm$ albite, and thicker exudation pods and lenses of quartz, commonly concentrated in axial portions of folds and in cross-cutting veins. Exceptionally graphite-rich layers approaching impure coal occur locally, as at the South Skagit Highway southeast of Sedro Woolley (Misch, 1977). This information, together with the highly quartzose-feldspathic composition, especially of the graywacke units, and the lack of volcanic clasts, indicates that the Darrington had a continental sialic source (Misch, 1976). The description does not preclude a marine depositional environment, however.

The conformably overlying Shuksan Greenschist, which is only sparsely present in the western foothill belt discussed here, represents an episode of widespread volcanic activity subsequent to the clastic depositional phase. Misch (1959, 1966, 1976) demonstrated the basaltic parentage of the greenschists and blueschists. On the northeast side of Day Lake, a thin greenschist unit is overlain by about 450 m of Darrington Phyllite. The phyllite is overlain by a 90 m zone in mutually intercalated greenschist, phyllite, blueschist, and hematite schist; mutual intercalation was first reported by Vance (1957) and, near the contact, by Jones (1959).

Main Outcrop Belt

The Shuksan Metamorphic Suite is exposed in a northward broadening belt from the Darrington area (Vance, 1957) to the shore of Samish Bay. Both the northeast and southwest limits of this outcrop belt coincide with the trace of the Shuksan Thrust or with its contacts with younger deposits (Misch, 1966, 1977). Between Samish Bay and the Nooksack North Fork in the Mt. Baker region, the phyllites disappear beneath the Chuckanut Formation.

At most localities, the Darrington Phyllite contains the record of multiple deformation. At a small quarry two miles southeast of Sedro Woolley, along the South Skagit Highway, Evans and Misch (1976, p. 1005) describe the internal structure thus: "The

various phyllites contain the record of an s_1, s_2, s_3 sequence. S_1 survives in some panels between s_2 planes. The dominant foliation s_2 parallels the axial plane of tight folds of s_1, with major transposition of phyllosilicate and graphite layers. Asymmetric open folding of s_2 has led to an oblique incipient s_3 with further transposition of graphite and some phyllosilicate."

Isolated Exposures of Shuksan Suite

The northwesternmost exposure of the phyllites below the Chuckanut Formation was reported by Miller and Misch (1963) at the southern end of American Sumas Mountain, south of the Boulder Creek fault. North of the fault, only slices of Yellow Aster Complex and associated sheared ultramafic rocks within the imbricate zone in the upper portion of the Church Mountain Thrust Plate attest to the former extent of the Shuksan Plate in that area, nearly to the root zone on the east (Misch, 1966).

Isolated exposures of the Shuksan Suite west of the main outcrop belt are present at Samish Island and possibly at Burlington Hill. At Samish Island, schistose graywacke, slaty siltstone, and phyllite crop out along the northern shoreline. Early paracrystalline, in part isoclinal folding in the unit is accentuated by quartz-rich bands and layers, now strongly strung out. Limbs of folds are stretched, and exudation lenses and pods of quartz $\pm$ albite occur in fold hinges. Sericite is a major constituent, along with albite and minor actinolite. No volcanic clasts were found. Fold axes trend about N70E. Fold trends, direction of yielding, overall lithology, and multiple deformation of the Samish Island rocks correspond with those occurring in the Darrington Phyllite at the south end of Chuckanut Drive. Northwesterly trending, widely spaced, cross-cutting "kink folds" are identical to those found in the Darrington Phyllite at most localities farther east (s_3 of Evans and Misch, 1976), and are interpreted as being formed during thrusting. The Merger Oil and Gas Co. well at the eastern end of Samish Island bottomed in "schist" presumed to be the phyllites (Livingston, 1958).

The western portion of Burlington Hill contains an actinolitic greenschist with minor crossite, and relict Ti-augite. The eastern portion of the hill is composed of phyllitic slates and fine-grained metagraywacke. These rocks were tentatively assigned to the Shuksan Plate (Misch, 1977), but were recognized as being atypical of the Shuksan Suite. Similar rocks have subsequently been found at several localities below the Shuksan Thrust in the outer foothill belt. Their correlation with known units remains in doubt, however.

Rocks of the Imbricate Zone

Tectonic slices of crystalline rocks associated with ultramafic rocks and certain metavolcanic and metasedimentary rocks of unknown correlation are included in this discussion of the Shuksan Thrust Plate. In many instances their occurrence as klippen or as imbricate slices in the upper portion of the underlying Church Mountain Thrust Plate is the only indication of the proximity of the Shuksan Thrust or of its former existence. Due to tectonic mixing and generally poor exposures, details along the Shuksan Thrust and within the imbricate zone cannot be worked out in the foothill belt as they can in the high country such as Mt. Tomyhoi and Red Mountain (Misch, 1962, 1966).

Slices of metaplutonic igneous rocks ranging in composition from gabbro to quartz diorite, here considered partly Yellow Aster and partly younger intrusions, occur at several localities in the Cultus-Table Mountain area south of the Skagit Valley; along the

southern end of Chuckanut Drive; and on Chuckanut Mountain (Figs. 2, 3, 4 & 5). At most localities, these rocks have been metamorphosed in the greenschist and/or blueschist facies, and subsequently in the prehnite-pumpellyite facies. In the Table Mountain area, for example, Lovseth (1975) described a polymetamorphosed quartz diorite which displays overgrowths of crossite on primary green and brown hornblende. A later low-grade assemblage includes pumpellyite, stilpnomelane, sphene, calcite, chlorite, and quartz (refer to sample 9, Fig. 2). The complex imbricate zone is also present along

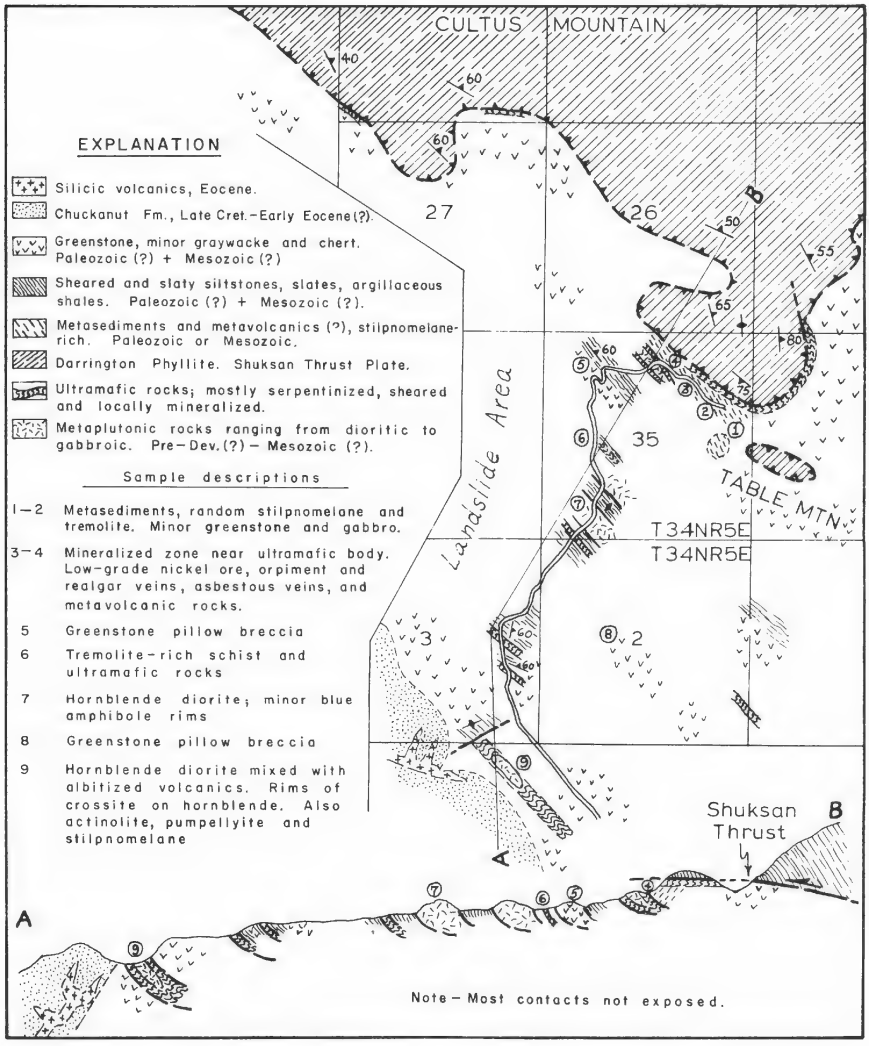
CULTUS MOUNTAIN
EXPLANATION
Silicic volcanics, Eocene.
Chuckanut Fm., Late Cret.-Early Eocene(?).
Greenstone, minor graywacke and chert. Paleozoic (?) + Mesozoic (?)
Sheared and slaty siltstones, slates, argillaceous shales. Paleozoic (?) + Mesozoic (?).
Metasediments and metavolcanics (?), stilpnomelane-rich. Paleozoic or Mesozoic.
Darrington Phyllite. Shuksan Thrust Plate.
Ultramafic rocks; mostly serpentinized, sheared and locally mineralized.
Metaplutonic rocks ranging from dioritic to gabbroic. Pre-Dev.(?) - Mesozoic (?).
Sample descriptions
1-2 Metasediments, random stilpnomelane and tremolite. Minor greenstone and gabbro.
3-4 Mineralized zone near ultramafic body. Low-grade nickel ore, orpiment and realgar veins, asbestous veins, and metavolcanic rocks.
5 Greenstone pillow breccia
6 Tremolite-rich schist and ultramafic rocks
7 Hornblende diorite; minor blue amphibole rims
8 Greenstone pillow breccia
9 Hornblende diorite mixed with albitized volcanics. Rims of crossite on hornblende. Also actinolite, pumpellyite and stilpnomelane
Landslide Area
TABLE MTN.
T34NR5E
T34NR5E
Shuksan Thrust
Note - Most contacts not exposed.

Figure 2. Imbricate zone below the Shuksan Thrust in the Table Mountain area.

the southern end of Chuckanut Drive and on Chuckanut Mountain. In many areas, both foliated and non-foliated rocks within the imbricate zone are characterized by abundant actinolite, and locally up to 60-70 percent stilpnomelane. Although not present everywhere, rocks containing such extremely high amounts of stilpnomelane appear to be more prevalent in the imbricate zone near the Shuksan Thrust; however, some of the greenschists within the overriding Shuksan Plate, in the Day Creek area, contain the same strong stilpnomelane overprint.

Ultramafic rocks, ranging from sheared serpentinites to massive, coarse-grained pyroxenites and peridotites, occur locally along the Shuksan Thrust contact, as well as along contacts between differing rock types within the imbricate zone. The presence of ultramafic rocks associated with basement slices of Yellow Aster was pointed out by Misch (1966, 1977) as being evidence for the deep-rooted nature of the Shuksan Thrust.

Several outcrops of metavolcanic and metasedimentary rocks are present in the imbricate zone in the Table Mountain area (Fig. 2), in the lowest Skagit Valley, and

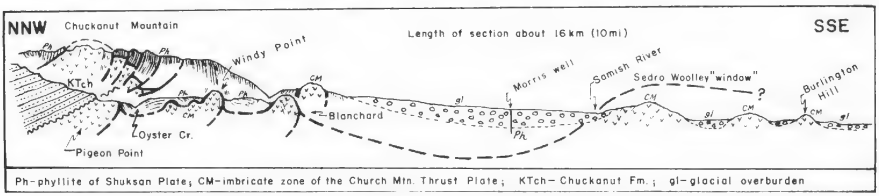

Figure 3. Diagrammatic sketch of interpreted folding, imbrication, and possible faulting of the Shuksan Thrust between the Skagit Valley and Chuckanut Mountain. Half-windows exposing the underlying Church Mountain Thrust Plate and the imbricate zone consist of presumed Chilliwack Group, slices of metaplutonic rocks, and sheared ultramafic rocks. Imbrication during thrusting possibly followed by folding and faulting predates Chuckanut deposition on the half-window at Oyster Creek. Later Eocene fold trends are parallel with the line of section shown here.

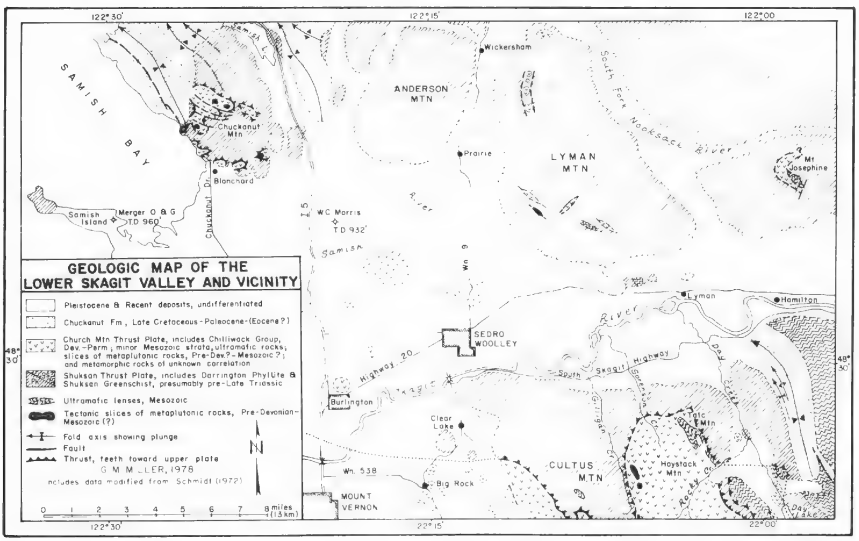

Figure 4. Geologic map of the lower Skagit Valley and vicinity.

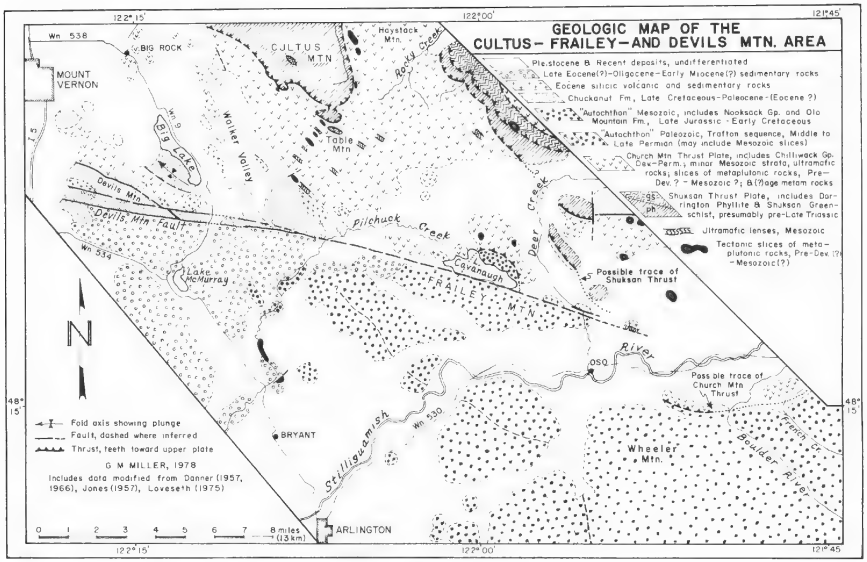
GEOLOGIC MAP OF THE
CULTUS– FRAILEY–AND DEVILS MTN. AREA
Pleistocene & Recent deposits, undifferentiated
Late Eocene(?)–Oligocene–Early Miocene(?) sedimentary rocks
Eocene silicic volcanic and sedimentary rocks
Chuckanut Fm., Late Cretaceous–Paleocene–(Eocene ?)
"Autochthon" Mesozoic, includes Nooksack Gp. and Olo Mountain Fm., Late Jurassic - Early Cretaceous
"Autochthon" Paleozoic, Tratton sequence, Middle to Late Permian (may include Mesozoic slices)
Church Mtn Thrust Plate, includes Chilliwack Gp. Dev–Perm., minor Mesozoic strata, ultramafic rocks; slices of metaplutonic rocks, Pre–Dev.? – Mesozoic ?; & (?)age metam rocks
Shuksan Thrust Plate, includes Darrington Phyllite & Shuksan Greenschist, presumably pre-Late Triassic
Ultramafic lenses, Mesozoic
Tectonic slices of meta–plutonic rocks, Pre-Dev.(?) – Mesozoic(?)
Possible trace of Shuksan Thrust
Possible trace of Church Mtn Thrust
Fold axis showing plunge
Fault, dashed where inferred
Thrust, teeth toward upper plate
G M MILLER, 1978
Includes data modified from Danner (1957, 1966), Jones (1957), Loveseth (1975)
0 1 2 3 4 5 6 7 8 miles
(13 km)
122°15'
122°00'
121°45'
48° 15'
Wn 538
BIG ROCK
MOUNT VERNON
CULTUS MTN.
Haystack Mtn.
Rocky Creek
Walker Valley
Big Lake
Table Mtn.
Devils Mtn.
Devils Mtn. Fault
Pilchuck Creek
Deer Creek
Lake McMurray
FRAILEY MTN.
Cavanaugh
OSQ
River
Stillaguamish
Wn 530
BRYANT
ARLINGTON
Wheeler Mtn.
Boulder Creek
Boulder River
N

Figure 5. Geologic map of the Cultus-Frailey-and Devils Mountain area.

in the Chuckanut Drive-Chuckanut Mountain area. These rocks are atypical of the Chilliwack Group although they may be units not previously recognized to the east. Some slates, slaty phyllites, and metagraywackes resemble the Mesozoic section. Slices of Mesozoic rocks, including Nooksack, are known in the Church Mountain Plate (Misch, 1966).

Trace of the Shuksan Thrust

As shown on Figures 4 and 5, the Shuksan Thrust can be mapped in several windows and half-windows in the Chuckanut Drive-Chuckanut Mountain area and, south of the Skagit Valley, in the Cultus Mountain-Day Creek area. Although the thrust contact is only locally exposed, the trace of the thrust can be closely delineated on the basis of the outcrop distribution.

Chuckanut Drive-Chuckanut Mountain Area

Exposures of sheared to massive greenstones, minor metasediments, metaplutonic, and ultramafic rocks are present in several half-windows below the phyllites between Blanchard and Pigeon Point (Miller, 1969). Beginning at Pigeon Point (Fig. 3) and extending eastward to the top of and down the east flank of Chuckanut Mountain, a large anticlinal half-window exposing rocks of the imbricate zone is unconformably overlain by the Chuckanut Formation on the west. Attitudes of the thrust contact range from moderate to nearly vertical, and show features of having been modified by both folding and faulting (Fig. 3).

On the south side of the Chuckanut Mountain half-window, vertical to steeply north-dipping shear zones parallel the N60-70W trend of schistosity within the overriding phyllites. Dominant ridges of the phyllites between stream valleys, plus offset of the thrust along stream valleys, indicate that the thrust contact is modified by faults.

Schmidt (1972) traced the contact between the Shuksan Metamorphic Suite and rocks which he assigned to the Yellow Aster Complex in the Chuckanut Mountain area. On the basis of outcrops within the imbricate zone along Chuckanut Drive, he erroneously concluded that the "Yellow Aster" on Chuckanut Mountain was thrust over the phyllites. Folding of the thrust during the Eocene orogeny accounts for the large half-window being exposed at the top and down both east and west flanks of Chuckanut Mountain. That is, Chuckanut Mountain east of Oyster Creek is along an anticline between the two synclines preserving the Chuckanut Formation as shown in Figure 4. Additional complications along the western base of Chuckanut Mountain may be due to Eocene deformation which in places produced local eastward thrusting (Miller and Misch, 1963; Misch, 1966; Heath, 1971).

Because two thrust plates are involved, imbrication of the lower plate could be reflected as extreme folding and/or imbrication within the upper plate during movement as diagrammed on Figure 3. Thus, the Shuksan Thrust would act in the same manner as a bedding plane between the Church Mountain Thrust Plate and the incompetent phyllites of the Shuksan Thrust Plate. Imbricate faults developed in the Church Mountain Plate could extend into the phyllites offsetting the thrust as on Chuckanut Mountain. At other places, the Shuksan Thrust might not be broken; rather, it would be folded and wrapped around the imbricate slices of the Church Mountain Plate such as along Chuckanut Drive. It appears that the imbrication and/or folding here took place during thrusting, but it could be the result of a later deformational event prior to the Eocene orogeny.

Cultus Mountain-Day Creek Area

On the west and south sides of Cultus Mountain (Fig. 5), the Shuksan Thrust is well exposed at several localities. Ultramafic rocks are present locally along the contact, within the phyllites of the thrust plate, and in the imbricate zone below. The thrust continues around the southern end of Cultus Mountain and trends northward into the headwaters of Gilligan Creek. The distribution of phyllites and imbricate zone rocks indicates that the thrust extends northeastward into the Sorenson Creek drainage. Further east, the thrust continues toward Talc Mountain. From Talc Mountain it trends southeasterly into Day Creek, forming a half-window open to the southeast. At one locality south of Talc Mountain, a slice of sheared greenstone overlying the phyllite along the thrust contact recalls the imbricate relations found along Chuckanut Drive. Ultramafic rocks are present along the contact at several places in the Talc Mountain and Day Creek area.

The half-window in the Haystack Mountain area was eroded in a northwesterly plunging Eocene anticline which parallels two flanking belts of synclinally preserved Chuckanut, one east of Day Creek, the other in Walker Valley on the west. This anticline may continue toward Chuckanut Mountain and cause the Sedro Woolley window.

Beginning at the ridge south of Rocky Creek and continuing southeastward toward Deer Creek, a thin band of phyllite is overlain by an estimated several hundred meters of greenschist with minor amounts of blueschist. Altered and sheared hornblende diorite, possibly Yellow Aster, near the contact plus the abnormally thin section of phyllites suggest a thrust contact between the phyllite and greenschist at this locality. The Shuksan Suite rocks appear to be slivers within the imbricate zone below the Shuksan Thrust, for they are bounded on the east by metasediments and -volcanics, albite-epidote-

amphibolites, and ultramafic rocks on the ridge south of Day Lake.

The belt of Shuksan Greenschist, actually a thick zone of greenschist with intercalated phyllites east of Day Creek, apparently is the western continuation of the large synclinal belt of this unit mapped by Jones (1959) and Vance (compare Huntting *et al.*, 1961) between Finney Peak and the Skagit Valley. A small outcrop of actinolitic schist on the north side of the Skagit Valley near Lyman is the northwesternmost exposure of this greenschist belt.

Farther southeast, between Deer Creek and Higgins Mountain, Jones (1957) mapped isolated occurrences of phyllite, Yellow Aster, Chilliwack, and ultramafic rocks in a possible continuation of the Shuksan Thrust and underlying imbricate zone. Tertiary faulting involving the Chuckanut Formation (Jones, 1957) may have offset the thrust in this area. The Shuksan Thrust is not exposed farther east between Deer Creek and Darrington, where Vance (1957) originally recognized the thrust.

Zones of Imbrication and/or Faulting within the Shuksan Thrust Plate

Small, discontinuous zones of serpentinized ultramafic rocks usually associated with slices of clinopyroxene-bearing metavolcanics, locally with quartz diorite and coarse-grained actinolite schist, occur within the phyllites of the thrust plate. These zones, or slivers, may represent imbrication during thrusting, or be due to later faulting and disharmonic movement during the Eocene folding of the thrust plate. The zones have been found on Lyman Mountain, Mt. Josephine, the Day Creek area, the east end of Lake Samish, and in the Chuckanut Mountain area. Their dips range from near vertical to moderate, mostly to the northeast, but one dips to the southwest.

Church Mountain Thrust Plate

Westernmost Exposures

North of the Skagit River, the eugeosynclinal Paleozoic Chilliwack Group and minor Mesozoic rocks of the Church Mountain Thrust Plate have been traced throughout the western flank of the North Cascades by Misch (1966, 1977). In the outer foothill belt, the westernmost exposures of rocks of similar lithology and structural position as the Church Mountain Plate and imbricate zone occur along the southern end of Chuckanut Drive (discussed earlier) and in the low hills east of Mount Vernon near Big Rock. In the Devils Mountain area, certain dacitic volcanic rocks and clastic sedimentary rocks may be of Mesozoic age and be "autochthonous," or be Mesozoic rocks within the imbricate zone of the Church Mountain Plate.

Haystack Mountain-Lake Cavanaugh Area

The outcrop belt of metasedimentary and metavolcanic rocks plus minor ultramafic and metaplutonic slices in the Haystack Mountain-Lake Cavanaugh area are considered part of the Church Mountain Thrust Plate. Rocks resembling both Chilliwack and Mesozoic types found farther northeast are present; others are of unknown correlation. The apparent mixture may be due to imbrication, or be due to units not present to the east. In the Haystack Mountain half-window, metamorphism ranges from incipient shearing to the production of phyllites and greenschists. Yielding is to the southwest. The degree of metamorphism in most but not all of the rocks, especially those not resembling the Chilliwack in the type area, is higher than that reported by Misch (1966, 1977) for the Church Mountain Plate; the significance of this fact is still to be worked out. Mesozoic-

appearing metasiltstones in Rocky Creek may be a window, but they are considered part of the imbricate zone.

Sedro Woolley Area

Outcrops of presumed Chilliwack Group rocks in the lower Skagit Valley, within the western limit of the Shuksan Thrust Plate, probably represent a window or half-window through the Shuksan Thrust in that area. The knob between Burlington and Sedro Woolley, for example, is composed of metamorphosed Chilliwack pillow basalts (Misch, 1977). North and northwest of Sedro Woolley several low knobs and ridges are composed of graywacke, siltstone, and greenstone. Northwest of these outcrops, the W. C. Morris well (Livingston, 1958) bottomed in "graphitic schist," presumably the Darrington Phyllite which is exposed farther northwest at Chuckanut Mountain (Fig. 3). The Sedro Woolley window or half-window probably represents a culmination along the Eocene anticline trending northwesterly from the Haystack Mountain half-window to Chuckanut Mountain.

Autochthon

Mesozoic Rocks

The thick Mesozoic section exposed in a window below the Church Mountain Thrust Plate in the region around Mt. Baker and in southernmost British Columbia has been described by Misch (1966). The Nooksack Group, of Late Jurassic-Early Cretaceous age, also has been reported by Danner (1957, 1966) 80 km farther south in the area north of the Skykomish Valley. Danner also described a belt of presumed Mesozoic rocks extending south from Frailey Mountain toward the Skykomish occurrence which may be in part a Nooksack equivalent.

The Nooksack Group in the northern portion of the area—Mt. Baker window to Lake Cavanaugh—as described by Misch (1966, p. 118), "has some flysch-like aspects and represents a period of rapid marine accumulation of clastics, probably largely in deep water, but with local tectonic highs. True clay sediments were minor, and quartz sands more or less absent. Graywackes commonly are very rich in volcanic clasts. Most of the wide-spread siltstones are 'micrograywackes' containing the same clasts as the coarser sediments. Calcareous admixture occurs in places." Misch further points out that conglomeratic rocks are minor; volcanic rocks are rare, mostly dikes and sills of dacite. No limestone or ribbon chert is known in the section, and quartz is very subordinate even in the graywacke units.

Small windows of typical Nooksack rocks below the Church Mountain Thrust Plate are present on the northeast side of Lake Cavanaugh and possibly in Rocky Creek, and probable Nooksack equivalents have been described near LaConner by Danner (1957) and have been reported by Misch (1966) on Lummi Island. More recently Vance (1975, 1977) has described the rocks on the southern half of Lummi Island, and similar rocks elsewhere in the San Juans; he has designated them as the Lummi Formation.

The Mesozoic sequence extending south from the Frailey Mountain area toward the Skykomish Valley, named and described by Danner (1957) as the Olo Mountain Formation and Sultan unit, contains volcanic rocks, ribbon cherts, and minor limestones. There is also a higher quartz content in some of the graywackes than in the typical

Nooksack Group farther north. Thus, the facies of the Mesozoic section is different toward the south or southwest, south of the Devils Mountain fault.

Paleozoic Rocks

South of the Devils Mountain fault, a belt of Paleozoic rocks extending southeastward from Pilchuck Creek to Mt. Pilchuck and beyond has been named and described by Danner (1966) as the Trafton sequence; it was originally termed the Stilliguamish Group (Danner, 1957). The Trafton consists of volcanic rocks, graywacke, siltstone, ribbon chert, and limestone. Without fossil evidence this sequence cannot be distinguished from the Chilliwack Group. Danner (1977) has shown that the Chilliwack Group, known to be in the Church Mountain Thrust Plate, contains a non-Tethyan faunal assemblage, whereas the Trafton sequence, as well as the Paleozoic rocks in the San Juan Islands, contains a Tethyan assemblage. Fossil finds by Whetten (1978 and pers. comm.) have demonstrated that both Paleozoic and Mesozoic rocks, as young as Jurassic, are present within rocks mapped as the Trafton sequence.

Deformation within the "Autochthon"

The degree of deformation within the "autochthon" is as intense as in the Church Mountain Thrust Plate. In both the Mesozoic and Paleozoic rocks, intense folding, locally isoclinal, shearing, and brecciation are common. The direction of yielding is southwestward, the same as in the overriding thrust plates. Contacts between major rock units are generally faulted as first observed by Danner (1957). Although these units are considered "autochthonous" relative to the Church Mountain and Shuksan Thrust Plates, their intense deformation, the apparent mixture of Paleozoic and Mesozoic rocks within the Trafton sequence, plus the occurrence of gneissose diorite to amphibolite in Pilchuck Creek (Jenkins, 1924; Danner, 1957, 1977), suggest the possibility of lower nonexposed thrusting in this region.

Offset of Thrusts by the Devils Mountain Fault

Rocks known to be in the same tectonic position as the Church Mountain Thrust Plate, as shown by the Lake Cavanaugh and (?) Rocky Creek windows, as well as the associated imbricate zone, can be traced southward to the Devils Mountain fault mapped by Hobbs and Pecora (1941), Miller (1961), and Lovseth (1975). As shown on Figure 5, the fault can be traced east-southeastward from Devils Mountain toward Lake Cavanaugh and possibly beyond Deer Creek. If the fault continues this trend toward Darrington it must die out, for major north-south trending structures such as the trace of the Shuksan Thrust, the Straight Creek fault east of Darrington (Vance, 1957), and the Darrington fault zone (Vance and Dungan, 1977; Vance, pers. comm.) are not offset. Whetten (1978) suggests that the fault curves to the southeast up the Boulder River.

In addition to the Church Mountain Plate, a thick section of the Chuckanut Formation (Weaver, 1937) unconformably overlain by silicic volcanics dated by Lovseth (1975) at 41 m.y., and intercalated sediments are recognized only north of the fault. East of Deer Creek, Shuksan Suite rocks are also present north of the fault.

South of the fault, the Chuckanut Formation has only been found at the western end of Devils Mountain, but neither the thrust plates nor the Eocene volcanics and sediments so far have been positively identified. South of the fault, outcrops of metabasalts near the mouth of French Creek and north of Wheeler Mountain (Fig. 5) are here tentatively

assigned to the Chilliwack Group and may be part of the Church Mountain Thrust Plate. The sequence of metabasalt, graywacke, chert, and argillaceous siltstone exposed on Frailey Mountain resembles part of the Church Mountain Plate to the north; however, they are also much like the Olo Mountain Formation to the south. For the present, the Frailey Mountain rocks are shown as being part of the "authochthon." To complicate matters, the thick sequence of interbedded conglomerates and finer-grained clastics including Late Eocene (?) and Oligocene to Early Miocene (Danner, 1975; Lovseth, 1975; and Miller, 1961) present south of the fault has not been found to the north. This fact indicates an opposite sense of displacement from that dictated by older units involved.

On the one hand, vertical displacement with little or no horizontal component along the Devils Mountain fault can account for the large offset of the thrust plates as well as for the younger stratigraphic units involved. This displacement requires an initial vertical movement in which the thrust plates, the Chuckanut, and the Eocene volcanic and sedimentary rocks are preserved on the down-dropped northern side, whereas a later, opposite displacement would be required to account for the Late Eocene (?) and Oligocene to Early Miocene sediments being preserved on the down-dropped southern side. On the other hand, Lovseth (1975) and more recently Whetten (1978) propose large left-lateral offset, up to 60 km, to account for relationships along the Devils Mountain fault.

There is no offset of the Shuksan Thrust which continues far to the southeast of the area discussed in this paper (Vance, 1957; Misch, 1966). If the fault curves to the southeast up the Boulder River drainage, as suggested by Whetten (1978), it would trend toward the system of west-dipping high angle faults described by Vance and Dungan (1977) as being early Oligocene in age and which "occurred prior to the intrusion of epizonal granodioritic plutons dated at about 34 m.y." (Vance and Dungan, 1977, p. 1497). Much more work needs to be done to establish firmly: (a) any pre-Early Miocene movement along the Devils Mountain fault; (b) the continuation and trend beyond the exposed portion of the fault; (c) the type and amount of movement of the fault; and (d) the existence of the Church Mountain Thrust Plate south of the fault.

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Drainage History of the Lewiston Basin

Abstract

Drainage development in the Lewiston Basin in northwestern Idaho and southeastern Washington is related to the volcanic and tectonic history of the area. Subsidence of the basin resulting from vertical movement or horizontal compression occurred during late Grande Ronde time, prior to the conclusion of eruption of the Columbia River Group lava flows. Major trunk streams established courses toward the basin during Wanapum time. Lacustrine conditions persisted until Saddle Mountains time when canyon-cutting began. Saddle Mountains "intracanyon" flows were erupted into ancestral canyons of the Snake and Clearwater Rivers. The Clearwater River occupied a position in a synclinal trough at the center of the basin. Initial faulting along the Clearwater fault zone caused the Clearwater River to shift its position north to the fault zone. The final "intracanyon" lava flow was erupted into channels of the Snake and Clearwater Rivers after the Clearwater's northward shift. Renewed faulting soon after the extrusion of the youngest "intracanyon" flow caused deposition of the Clarkston Gravels and readjustment of the channels of the Snake and Clearwater Rivers.

Physiographic Description

The Lewiston Basin is a structural and topographic depression, approximately 60 km long and 30 km wide, located in northwestern Idaho and southeastern Washington (Fig. 1). At the topographic low point of the basin the Clearwater River joins the Snake River. The Snake River enters and leaves the Lewiston Basin along a northwest-trending course.

Within the basin, the Clearwater River flows west along the base of a prominent linear escarpment, the Clearwater Escarpment on the north. Near Lewiston, relief along the escarpment is approximately 700 m. To the south, the basin rises gradually to meet the Waha Escarpment, another steeply sloping prominent topographic feature.

Both the Snake and Clearwater Rivers enter the Lewiston Basin through deep, steep-walled canyons, which reach depths of 1500 m; at the center of the basin, these rivers flow in valleys less than 40 m deep. The north-trending course of the Snake River makes an abrupt 90 degree turn to the west, near Lewiston, at the point where it reaches the Clearwater Escarpment. The Snake then flows 13 km westward along the base of the escarpment (Fig. 2), where it makes another 90° turn as it crosses the Clearwater Escarpment and leaves the Lewiston Basin to follow a northwesterly course through a deep canyon. The cities of Lewiston, Idaho, and Clarkston, Washington, are located near the confluence of the Snake and Clearwater Rivers, on opposite sides of the Snake.

Stratigraphy of the Columbia River Group

Prior to the extrusion of the lavas of the Columbia River Group during Miocene time, the Lewiston region was characterized by rugged, mountainous topography. Drainage, consisting of streams flowing in deeply eroded canyons, was primarily from east to west (Bond, 1963).

During Miocene time, basalt flows erupted from northwest-trending linear dike

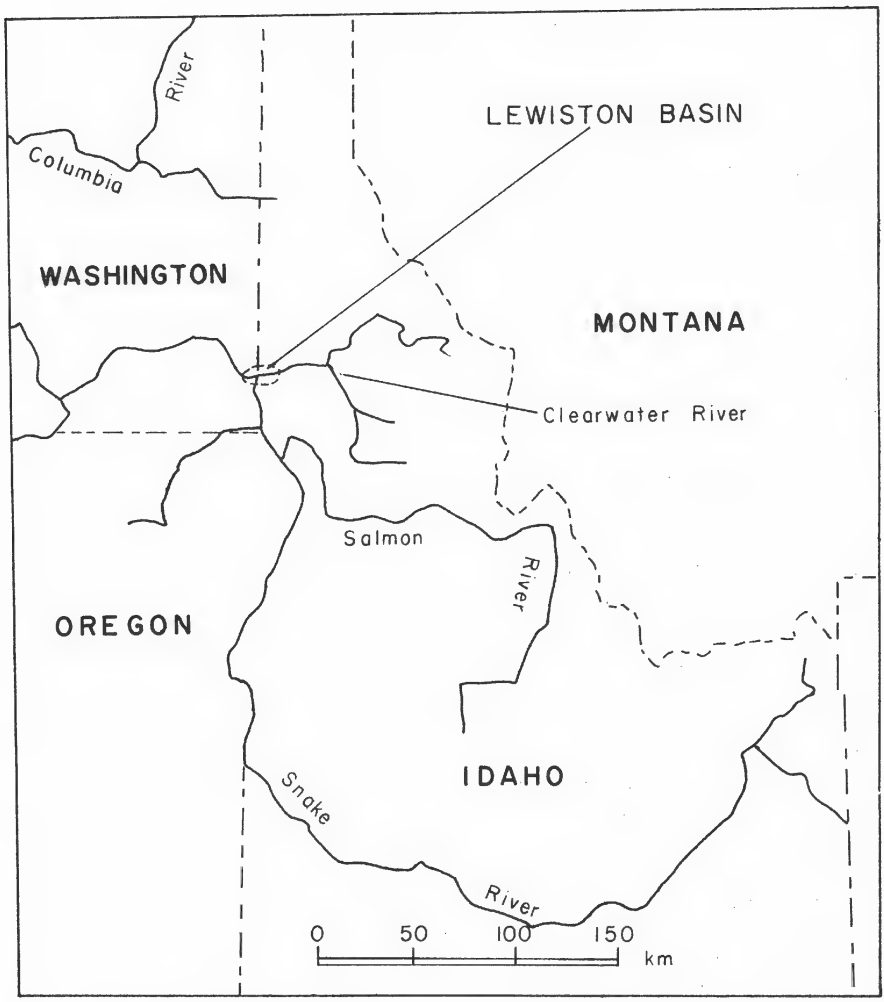

Figure 1. Map of a portion of the northwestern United States showing location of the Lewiston Basin.

swarms into a subsiding basin between the Cascade and Rocky Mountains. Most of the flows were confined to the central portions of the basin in central and south-central Washington and north-central Oregon. Three large lobes of lava flows advanced eastward into northern Idaho. The central lobe, or embayment, which now contains the Lewiston Basin, is known as the Clearwater Embayment.

Recent chemical, petrographic, paleomagnetic, and field studies have led to a four-fold stratigraphic subdivision of the Columbia River Group (Wright *et al.*, 1973). The lowest formation in the Columbia River Group consists concurrently of the Picture Gorge Basalt in central Oregon and the Imnaha Basalt (Hooper, 1974) in northern

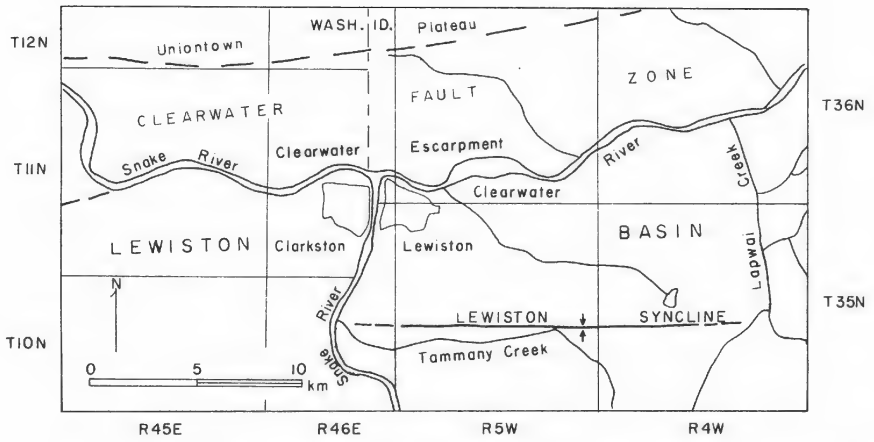

Figure 2. Map of the central part of the Lewiston Basin showing present drainage, major physiographic features, and locations of the Clearwater fault zone and the Lewiston syncline. The southern boundary of the Clearwater fault zone coincides approximately with the Clearwater River and the portion of the Snake River west of the confluence.

Idaho (Fig. 3). Above the Picture Gorge and Imnaha Basalts lies the Yakima Basalt Subgroup and associated sedimentary interbeds, which Wright *et al.* (1973) divide into informal lower, middle, and upper units. Swanson *et al.* (in press) have assigned the names Grande Ronde Basalt, Wanapum Basalt, and Saddle Mountains Basalt to replace the informal terms lower Yakima Basalt, middle Yakima Basalt, and upper Yakima Basalt respectively. Areally, the Grande Ronde Basalt (Fig. 3) is the most widely occurring stratigraphic unit of the Columbia River Group.

Camp (1976) discusses the stratigraphy of the basalt flows in the Lewiston Basin and describes ten flows within the Wanapum and Saddle Mountains Basalts. Local subsidence of the Lewiston Basin probably began in late Grande Ronde time (Camp, 1976). The subsidence may have been caused by epeirogenic or isostatic adjustment resulting from basalt extrusion, or an episode of deformation, which continued throughout and after the period of volcanism. This subsidence resulted in the establishment of drainage toward the Lewiston topographic basin. Lacustrine conditions in the basin were initiated because of the lack of an initial drainage outlet. Fluvial-lacustrine interbeds were deposited between flows of the Wanapum and Saddle Mountains units in the Lewiston Basin (Camp, 1976). The thickest interbed, the Sweetwater Creek Interbed (Fig. 3), overlies the widespread Lolo Member of the Wanapum Basalt, and attains a maximum thickness of 70 m near the center of the basin. Above the Sweetwater Creek Interbed lie the "Uniontown" flows (Fig. 3), a group of five flows erupted from a northwest-trending dike system northwest of the Lewiston Basin (Swanson, Wright, and Helz, 1975; Camp, 1976). The presence of a fluvial-lacustrine interbed above each "Uniontown" flow indicates that lacustrine conditions persisted in the Lewiston Basin during the eruption of these flows. After eruption of the "Uniontown" flows, lacustrine conditions ended and the rivers flowing into the basin began to erode canyons. The final three Saddle Mountains flows are known as "intracanyon" flows (Fig. 3) because their outcrops are limited to these ancestral canyons of the Snake and Clearwater Rivers. The

"intracanyon" flows were assigned to Pleistocene age (Lupher and Warren, 1942; Bond, 1963), but were recently reinterpreted as being a continuation of Columbia River volcanism during late Miocene and possibly early Pliocene time (Swanson, Wright, and Clem, 1975; Camp, 1976). The Clarkston Gravels—thick, cemented fluvial gravel deposits that overlie the "intracanyon" flows within the ancestral canyons—are also considered to be Miocene-Pliocene in age rather than Pleistocene (Fig. 3).

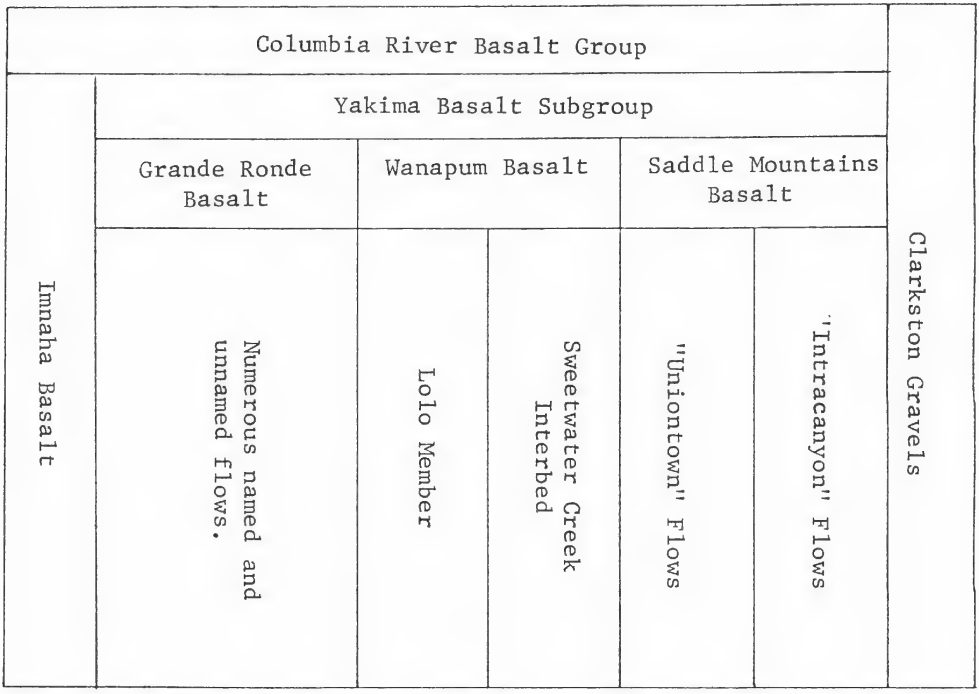

Figure 3. Generalized stratigraphy of the Columbia River Group in the Lewiston Basin.

Structure

The Clearwater Escarpment (Fig. 2), forming the north end of the Lewiston Basin, has long been recognized as a major structural discontinuity (Russell, 1901). Russell concludes that the structure is a monoclinal fold formed by differential vertical movements of the lava plateau. Steep, southward-dipping lava flows along the Clearwater Escarpment near Lewiston bounded by near horizontal flows to the north in the Uniontown Plateau and to the south in the Lewiston Basin seem to support this interpretation. Other investigators mapping structures along the Clearwater Escarpment postulate that the structures are the result of both differential vertical movements and horizontal compression (Graham, 1949; Hollenbaugh, 1959; Camp, 1976). Camp interprets the structures along the Clearwater Escarpment as an anticlinal horst. The major fault along the escarpment, the Wilma fault (Graham, 1949), is present in and along the channel of the Snake River, extending westward from Lewiston to the western extent of the basin. The Wilma fault displacement is responsible for the difference in elevation

between the area south of the escarpment (Lewiston Basin) and the higher Uniontown Plateau to the north. Camp (1976), in agreement with previous investigators (Graham, 1949; Hollenbaugh, 1959), suggests that the structures along the Clearwater Escarpment decrease in amount of displacement to the east of Lewiston and are modified, becoming a simple monocline.

Kehew (1977) describes the continuation of the Wilma fault to the east of the Lewiston area, and explains other related structures which confirm that, although deformation does decrease in severity to the east, the Clearwater Escarpment constitutes a zone of complex faulting and folding. This disturbed zone extends at least 25 km east of Lewiston, and probably further. Kehew (1977) proposes that this fault zone along the Clearwater Escarpment be known as the Clearwater fault zone (Fig. 2) in order to emphasize the complexity of the deformation and the continuity of the structures previously mapped near Lewiston with those to the east. East of Lewiston, the fault zone does *not* terminate in a monocline as formerly interpreted: instead, it becomes a complex arrangement of tilted blocks, bounded by east and north to northwest-trending fault systems.

Features of the Clearwater fault zone suggest both horizontal compression and vertical movement. Minor folds along the western portion of the fault zone suggest compression, although the relative displacement of the Lewiston Basin with respect to the Uniontown Plateau to the north is downward across the fault zone. It seems most likely that a single continuous process of deformation produced the structures present, and that this process was dominantly compressional, at least in the Lewiston Basin area.

Drainage Development

Stratigraphic evidence indicates that subsidence of the Lewiston Basin began during late Grande Ronde time (Camp, 1976). The presence of fluvial-lacustrine interbeds within the Wanapum and Saddle Mountains sequence in the Lewiston Basin indicates that the subsidence of the basin resulted in the establishment of drainage toward the basin and the initiation of lacustrine conditions at the center of the basin. Evidence indicates that the Snake River at this early period was established along a structurally developed path to the Lewiston Basin. The ancestral Snake was a much smaller drainage system, having not yet captured the southern half of its present drainage basin at the oxbow bend site in the Seven Devils Mountains (Wheeler and Cook, 1954) in Hells Canyon to the south.

In a similar fashion, initial subsidence of the Lewiston Basin caused establishment of an ancestral Clearwater River system toward the basin. Streams flowing west from the mountainous areas to the east of the Lewiston Basin were initially dammed by lava flows advancing eastward. Eventually, an integrated drainage system was formed. The ancestral Clearwater River probably entered the basin along a structural trough which at that time formed the low point of the basin. This trough corresponds to the Lewiston syncline mapped by Bond (1963) (Fig. 2). Today, the Clearwater River flows in a seemingly anomalous position approximately 10 km north of the synclinal axis, along the north limb of the syncline. Figure 4 shows the postulated early position of the ancestal Clearwater River. The valley of Tammany Creek, a minor tributary of the Snake, occupies this synclinal axis. The valley of Tammany Creek (Fig. 5) is much wider than a stream the size of Tammany Creek could erode. Hollenbaugh (1959) suggests that the width of Tammany Creek valley is a result of rapid erosion of the weak Sweetwater

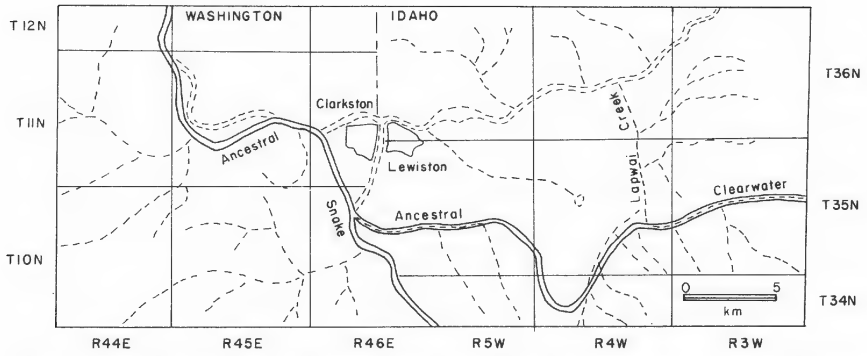

Figure 4. Early drainage in the Lewiston Basin. Solid lines show approximate courses of the ancestral Snake and Clearwater Rivers in Saddle Mountains time, after initial subsidence or downfolding of the Lewiston Basin. The ancestral Clearwater followed a course along the approximate synclinal axis of the basin. The Snake followed a course southwest of the site of Clarkston. Present drainage is shown as dashed lines.

Figure 5. View southeast up Tammany Creek valley. Width and position of valley suggest that the valley was eroded by early drainage from the east to the Lewiston Basin (ancestral Clearwater River).

Creek Interbed. However, other streams comparable in discharge and drainage basin area, which have also eroded their valleys through resistant lava flows downward into the Sweetwater Creek Interbed, have produced narrow V-shaped valleys in strong contrast to Tammany Creek valley. Barbed tributaries of Lapwai Creek (Fig. 4), and the east-west segment of Lapwai Creek itself, support the interpretation of a major stream in the position shown in Figure 4.

The Clearwater and Snake Rivers remained in the position shown in Figure 4 through Wanapum time. Canyon-cutting began after the eruption of the "Uniontown" flows of the Saddle Mountains Basalt, and the first two of the three Saddle Mountains "intracanyon" flows were erupted into these ancestral canyons. These intracanyon flows caused no major drainage changes.

Soon after the eruption of the first two intracanyon flows, initiation of faulting

occurred along the Clearwater fault zone, lowering the Lewiston Basin relative to the elevation of the area north of the fault zone. This event caused major alterations to the drainage system in the basin. The Clearwater River shifted, probably by headward erosion and capture, to a position within the fault zone (Fig. 6). The location of the Clearwater River within the Clearwater fault zone indicates that the Clearwater is not antecedent, but attained its location as a result of adjustment following faulting. Headwater erosion by Lapwai Creek (Fig. 6) beheaded part of the former drainage network of the Clearwater. During this episode of deformation, the Snake River maintained its previous northwesterly trend, southwest of the city of Clarkston (Fig. 6). Faulting offset exposures of the first two "intracanyon" flows. The final "intracanyon" flow entered the new channel of the Snake and Clearwater Rivers after the shift, suggesting that faulting began prior to the close of volcanism.

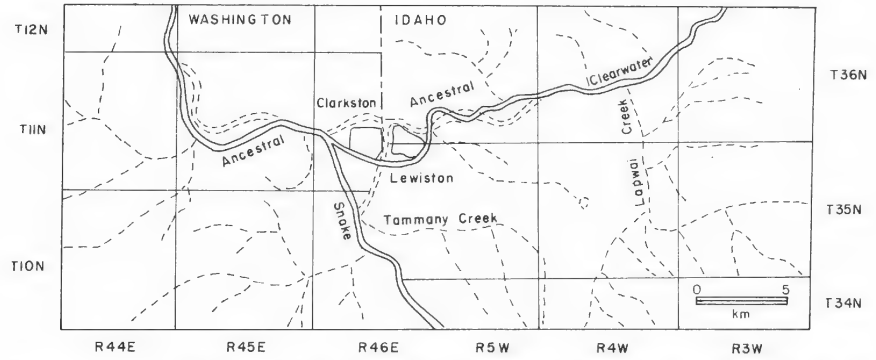

Figure 6. Shift of ancestral Clearwater to position along the Clearwater fault zone after faulting began just prior to the close of Columbia River Group volcanism. Continued lowering of the basin along the fault zone caused deposition of the Clarkston Gravels in the channels shown as solid lines in the central portions of the basin. Present drainage is shown as dashed lines.

Renewed or continued faulting along the Clearwater fault zone after the eruption of the last "intracanyon" flow caused the final series of major drainage adjustments. Lowering of the basin by faulting resulted in rapid aggradation by the streams near the center of the basin, filling the pre-existing channels with the Clarkston Gravels. When the channels were filled, the streams were free to migrate laterally and establish new positions. After the channels were filled with the Clarkston Gravels, channel locations (Fig. 6) shifted to new positions (Fig. 2). The position of the Clearwater River before the final shift (Fig. 6) was determined by tracing remnants of the last "intracanyon" flow and the Clarkston Gravels (Kehew, 1977). Thus, the Snake shifted to the east as described by Lupher (1945), and the Clearwater moved to its present channel just south of the previous orientation. Within the fault zone, minor streams adjusted by establishing courses along minor faults trending north-south or northwest-southeast.

River positions shown in Figure 2 are essentially those of the present. Following the drainage adjustments described above, canyons were progressively deepened during Pliocene and Quaternary time. The duration of the deformation of the area after Columbia River Group volcanism is not known. During Pleistocene time, two catas-

trophic floods moved through the Lewiston Basin (Kehew, 1977). The Bonneville Flood, caused by the spillover of pluvial Lake Bonneville in the Pleistocene, produced torrential waters flowing northward into the Snake River drainage (Malde, 1968). These floods resulted in large discharges of water moving through the Lewiston Basin from south to north. The flood waters deposited coarse gravels along the channel of the Snake River in the Lewiston Basin. At a later time, flood waters from the Glacial Lake Missoula flood moved up the Snake River from the channeled scabland region in central and eastern Washington into the Lewiston Basin. This flood deposited rhythmically bedded sand and silt on the lower slopes of the basin, indicating a depth of water in the basin of approximately 130 m.

Conclusion

Drainage history in the Lewiston Basin must be considered in relation to the volcanic and tectonic events that affected the area. The most important factor in the development of drainage in the basin was the structural deformation. The confluence of the Snake and Clearwater Rivers occurs at the center of the Lewiston Basin because of early structural depression of the basin. Once streams became established within the subsiding basin, their positions were altered in response to increasing deformation of the basin.

Development of the Clearwater fault zone was the dominant influence upon the location of the Clearwater River. The initial path of the Clearwater River to the basin was the synclinal axis at the center of the basin now occupied by Tammany Creek. The river eroded a wide channel in this position through several resistant lava flows. Activation of displacement along the Clearwater fault zone led to the development of an ancestral Clearwater River along the fault zone. The Clearwater River follows the fault zone to the confluence with the Snake. At the confluence, the Snake turns to follow the fault zone to the western edge of the basin.

The final shift of the river positions was the indirect result of continued fault displacement along the Clearwater fault zone. Faulting prior to the final shift lowered the local base level of the streams and caused rapid aggradation near the center of the basin. After this deposition filled the existing valleys, both the Snake and Clearwater Rivers adjusted their locations by lateral migration and began to erode their present channels.

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Chironomid Remains in Recent Sediments of Lake Washington

Abstract

The vertical distribution of chironomid remains in the sediment of Lake Washington was determined in each centimeter of a core 35 cm long taken from a depth of 63 m in 1975. The time covered is nearly 100 years, and thus includes the period of eutrophication and recovery. More than 900 individuals representing 51 taxa were found, most of them of littoral and sublittoral origin. *Protanypus* sp. and *Heterotrissocladius* sp. were more frequent in older sediments, whereas *Phaenopsectra* sp. was more frequent in younger sediments. The differences were small, and the results show that the bottom fauna did not respond to eutrophication with major changes in species composition.

Introduction

A sedimentary record of the eutrophication of Lake Washington and the lake's recovery after diversion of sewage has been demonstrated to exist as vertical variations in the composition of diatom remains (Stockner and Benson, 1967), pigments of bluegreen algae (Griffiths and Edmondson, 1975), and chemical properties of the sediments (Shapiro *et al.*, 1971; Edmondson, 1974). The preserved larval head capsules of midges of the family Chironomidae are very useful indicators of past changes in the condition of a lake (Deevey, 1942; Frey, 1964; Hofmann, 1971; Warwick, 1974). Although knowledge of the present chironomid fauna of Lake Washington is far from complete, a survey of the chironomid remains in the recent sediments was judged as worthwhile in view of the well documented changes in the lake during the last 60 years.

Lake Washington experienced two periods of eutrophication, the second with treated sewage effluent in the period 1941-1968 (Edmondson, 1972). Concentrations of oxygen in the hypolimnion in late summer remained above 3 mg/l most of the time, and anaerobic conditions did not develop for prolonged periods in a large part of the lake. Thus large qualitative changes in the hypolimnetic fauna based on oxygen requirements would not be expected, although species with specialized food requirements might be expected to change since the character of the phytoplankton varied greatly.

Methods

The core (Laboratory No. 61C) was taken on 5 February 1975 with an automatic piston corer, 35 mm in diameter, at 63 m depth in the central part of Lake Washington, near the western shore (point MP in Shapiro *et al.*, 1971). The sediment was cut in slices 1 cm thick and treated according to methods slightly modified from Hofmann (1971) After boiling with 10 percent KOH in a water bath for 10-20 minutes, the sample was diluted with water and allowed to settle. The water was decanted and 10 percent HCL added. After a few minutes, the sample was sifted through a 0.22 mm net. The sieved remains were carefully washed with water and transferred to a petri dish and sorted under a binocular at 25 times magnification or more. All remains of chironomid larvae

were passed through absolute ethanol and Cedar wood oil and mounted as permanent slides in Canada balsam.

Some fairly complete head capsules were found, but most of the material was heavily fragmented and the identification had to be made from the structure of the mentum only. For this reason, and because of the lack of comparative recent larval material from the littoral part of the lake, some of the genera within the Tanytarsini, Orthocladiinae, and Tanypodinae could not be positively identified.

Results and Discussion

Altogether 950 individuals were recovered from the uppermost 35 cm of the core. The material was surprisingly diverse with 51 different taxa (Table 1). From the large number of taxa found in this limited material, a comparatively large total number of chironomid species in Lake Washington may be postulated.

The great diversity as well as the specific composition of the fauna makes it clear that most of the chironomids found originate from much more shallow areas than the actual sampling site. Of the fifty-one taxa encountered only five, namely *Chironomus*, *Procladius*, *Phaenopsectra*, *Heterotrissocladius*, and *Protanypus*, belong to the fauna of the deep profundal (Thut, 1969; and Wiederholm, unpub. data). About 20 percent of the chironomids found in the core belong to these genera. Since most of them occur also in shallow areas, considerably more than 80 percent of the material may be expected to be the result of redeposition of material from littoral, sublittoral, and more shallow profundal areas. The three dominating genera, *Stempellina*, *Tanytarsus*, and *Cladotanytarsus*, are mostly littoral in their occurrence. Also, the somewhat less frequent *Polypedilum*, *Dicrotendipes*, *Cladopelma*, and *Paratanytarsus* are most numerous on littoral and sublittoral bottoms.

A remarkable fact is that no specimens of *Stictochironomus*, a regular member of the profundal communities in the eastern part of the lake (Thut, 1969), have been found in the present material. This further underlines the littoral character of the subfossil chironomid fauna.

The abundance of chironomids varies greatly with depth (Fig. 1). Except for the maximum between 12 and 13 cm, which is more than twice the number found at the second highest level, the total number of head capsules seems to be generally higher in the lowest part of the core. The numbers in the upper 9 cm and especially the uppermost 5 cm are remarkably low. No head capsules at all were found in the first and third cm of sediment.

A comparison of the different genera shows that the various peaks reflected in the total number of chironomids are consistent for nearly all taxa. Consistently higher numbers were found at 9-10, 12-13, and 18-20 cm depth. Many taxa show peaks also at 29-30 and 32-34 cm depth. This covariation among a great number of species proves that the head capsules are not randomly distributed along the vertical profile. Instead the variations in numbers must reflect specific events in the lake. These events may be of local character or include the whole lake.

In view of the strongly littoral character of the material as a whole, factors affecting the shallow areas of the lake should be considered first. Among these are currents, waves, and seiches, which may exert an eroding effect on the littoral and sublittoral bottoms resulting in transport and redeposition of sediments into deeper areas. One of the main

TABLE 1. Numbers of chironomids in the upper 35 cm of a core taken from Lake Washington in February, 1975.

	Numbers found	% of total
Stempellina	94	10
Tanytarsus	85	9
Cladotanytarsus	76	8
Procladius	71	8
Polypedilum	62	7
Chironomus	60	6
Dicrotendipes	57	6
Cladopelma	37	4
Paratanytarsus	35	4
Tanytarsini, unidentif.	33	4
Pentaneurini part.	27	3
Heterotrissocladius	26	3
Glyptotendipes	20	2
Protanypus	18	2
Orthocladiinae, unidentif.	14	1
Limnophyes	14	1
Tanypodinae, unidentif.	13	1
cf. **Cricotopus**	13	1
Psectrocladius	12	1
Micropsectra	12	1
Paraphaenocladius	11	1
Nilodorum	11	1
Paratendipes	11	1
Phaenopsectra sp. A	10	1
Phaenopsectra sp. B	10	1
Pseudochironomus	10	1
Endochironomus	9	< 1
cf. **Orthocladius**	8	< 1
Microtendipes	8	< 1
Parachironomus	8	< 1
cf. **Chaetocladius**	7	< 1
Chironomini, unidentif.	7	< 1
Labrundinia	6	< 1
Pseudosmittia	5	< 1
Zavrelia	5	< 1
Parakiefferiella sp. B	4	< 1
Phaenopsectra sp. D	4	< 1
Parakiefferiella sp. A	3	< 1
Orthocladiinae sp. H	3	< 1
Cryptochironomus	3	< 1
Phaenopsectra sp. C	3	< 1
Constempellina	3	< 1
cf. **Corynoneura**	2	< 1
Eukiefferiella	2	< 1
Monodiamesa	1	< 1
Unknown genus near **Paracricotopus**	1	< 1
? **Bryophaenocladius**	1	< 1
Cricotopus (Isocladius)	1	< 1
Orthocladiinae sp. G	1	< 1
Cryptotendipes	1	< 1
? **Fleuria**	1	< 1
Pagastiella	1	< 1
Stenochironomus	1	< 1
Unknown gen. Chironomini	1	< 1
Tanypodinae	117	12
Diamesinae	19	2
Orthocladiinae	128	14
Chironominae, Chironomini	336	35
Chironominae, Tanytarsini	343	36
Unidentified	7	< 1
	950	100

events in the recent history of Lake Washington was the lowering of the level in 1916 by 3.3 m. X-radiographs taken of the present core before slicing show that this date is reflected as a strong lamination extending from 24.5 to 27.5 cm in the core.

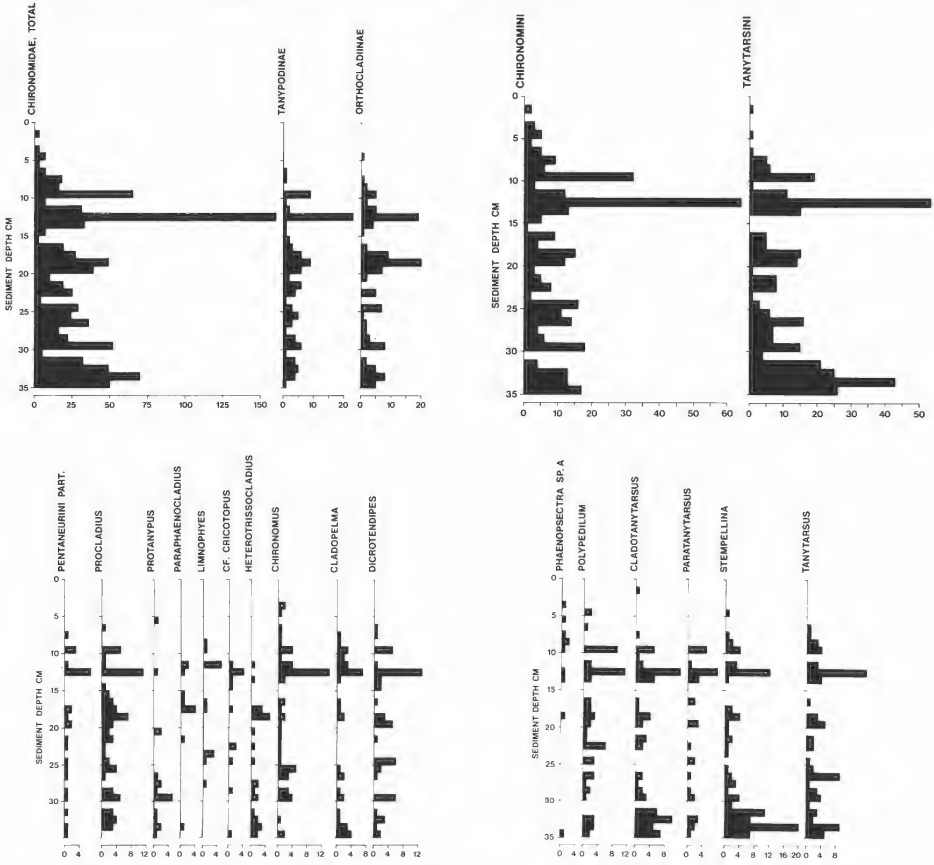

Figure 1. Vertical distribution of chironomids within the sediment core mentioned in Table 1; numbers per cm length of core. The levels 5, 6, 11, and 16 cm may not be strictly quantitative as a result of initial difficulties in the sorting.

The effect that might be expected on the number of fossil chironomids from the lowering of the lake is not clear. The increased erosion of the newly exposed littoral areas may increase the deposition of inorganic material on deeper bottoms, but the animal remains previously deposited in these areas should also be transported to the deeper bottoms. The picture is also complicated by the fact that physical changes after lowering of the lake may have changed production of chironomids during the period of stabilization of the new littoral bottoms and their colonization.

Edmondson and Allison (1970) found several prominent laminations in X-radiographs of cores from the same area of Lake Washington. They assumed that many of them resulted from some event or condition that temporarily increased the local input

of silt relative to organic matter, but these events could not be identified. Most of the banding in the upper part of the cores results from layers dominated by diatoms alternating with layers dominated by silt and iron hydroxide. Presumably this alternating reflects seasonal changes in deposition, each clear diatom layer representing a spring bloom (Edmondson, 1974; and pers. comm.). Some cores have occasional X-ray absorptive layers that contain silt, possibly as a result of unusual events of redeposition of littoral material. In the present core, the X-radiograph shows layers from 9.5-10.0 cm, 13.5-14.5 cm, and in a thin layer at 18 cm. These correspond to peaks on the total chironomid curve within 1 cm.

Few clear indications of the periods of eutrophication are shown by the chironomid remains, largely because littoral and sublittoral species comprise the bulk of the material. These species are less useful as indicators of the lake's trophic state than those of the profundal communities. The sedimentary record is also blurred by the effects of the supposedly littoral events discussed above.

Some indication of general changes in the lake compared to earlier periods may, however, be found in the material. Among the specific indicator organisms, the genera *Protanypus* and *Heterotrissocladius* are more frequent in the layers deposited more than 75 years ago, (i.e., below 25 cm depth) than in the more recent material. Members of these genera are primarily restricted to oligotrophic lakes (cf. Sæther, 1975, Table 1). Also, *Phaenopsectra* sp. is more frequent above 15 cm depth of sediment. Species within this genus occur more frequently in more productive lakes than do those of the previous genera. Further, the percentage of *Chironomus* sp. is greater in the upper half of the core than in the lower part. Species of *Chironomus* are associated with mesotrophic-eutrophic conditions when occupying a dominant position in the chironomid fauna. The changes in vertical stratification referred to above are consistent with the known changes in the lake, although the numbers of each taxa are small except for *Chironomus.*

As for the representativeness of the single core studied, it may suffice to cite Griffiths & Edmondson (1975), who, after analysis of pigments in several cores from the actual sampling site, wrote: "The general pattern of the oscillaxanthin profiles are again strikingly similar, which should lend encouragement to investigators who have to interpret data from single cores . . . ." Cores from a more central part of the lake may show a lower proportion of littoral and sublittoral taxa, but major changes in the chironomid fauna, had they occurred, would no doubt show up also in the area studied here.

The scarcity of remains in the top 5 cm must be in part related to the fact that the sediment has not fully compacted, and represents a smaller time of accumulation than a similar thickness of deeper sediment. Cores in this area of the lake have about two-thirds the dry weight content in the top 5 cm as in the next 5 cm. The difference in abundance of remains, however, is not proportional to the time of accumulation. The possibility exists that the production of littoral chironomids has been reduced since the diversion of sewage.

In summary, while the bottom fauna of Lake Washington changed during periods of eutrophication and de-eutrophication, changes in composition of taxa were relatively small. Subtle shifts in species composition may have occurred, but these changes did not reach the level of exclusion of whole genera or a pronounced increase in abundance of others. This condition may be attributed largely to the fact that eutrophication was not

permitted to reach the point of generating anaerobic conditions in the hypolimnion, and that enrichment lasted relatively few years.

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Air Pollution and the Distribution of Corticolous Lichens in Seattle, Washington

Abstract

Lichen species were sampled at 85 sites within the city of Seattle. These data, expressed numerically, were used to construct a map consisting of five zones which reflected variances in the composition of the lichen flora along air pollution gradients. The topography of the city, land use patterns, and prevailing winds were found to affect the dispersion of air pollutants and therefore the distribution of lichen species.

Introduction

As early as the mid-nineteenth century botanists were aware that lichens and bryophytes were scarce in the neighborhood of large cities. They recognized that air pollution could affect the establishment and development of these organisms. Subsequent studies have correlated the distribution of lichen species with increased air pollution (Showman, 1975; Brodo, 1967; Laundon, 1967). As a result of such studies, it has been widely accepted that the lichen vegetation in cities is adversely affected.

Air pollution in and around urban centers reaches concentrations high enough to have a detrimental effect on vascular plants (Nash, 1973). Evidence also indicates that lichens are extremely sensitive to air pollution, and that the degree of sensitivity can vary among species. Lichens accumulate minerals as well as pollutants efficiently. They are slow growing and long lived and can therefore accumulate large quantities of toxic materials over a long period of time, whereas other plant types usually shed large areas of toxin-laden foliage each season (Brodo, 1967). Vascular plants are also at an advantage because they are protected by both cuticle and stomata.

Of the pollutants resulting from fossil fuel combustion, sulfur dioxide has been found to affect lichen growth to the greatest extent. Studies by Baddeley, Ferry, and Finegan (1972), Coker (1967), Showman (1972), Rao and Le Blanc (1966), and Richardson and Puckett (1973) have shown how sulfur dioxide affects lichen metabolism. These studies have also revealed varying tolerances among lichen species. Other pollutants such as fluroide, peroxyacetyl nitrate (PAN), and heavy metals are also detrimental to lichens. However, sulfur dioxide is the most important pollutant on a worldwide basis.

Since lichens are found to be very sensitive to sulfur dioxide when compared with higher plants, and species vary greatly in their sensitivity, they have considerable potential as biological indicators of sulfur dioxide levels. The value of living organisms rather than manmade instruments for assessing sulfur dioxide levels is that they are cheap and give an instant result—the presence or absence of species as a response to sulfur dioxide concentrations. However, lichens are much more sensitive and complex indicators than even the most sophisticated recording instruments, and will react to

many other environmental factors. They are a unique tool available to us in our quest to discover the extent of man's impact on the biosphere. The application of lichen mapping techniques on a large scale will provide us with data that can be useful over long periods of time in comparing the extent of sulfur dioxide pollution in the environment.

The objective of this study is to apply established lichen mapping techniques to the city of Seattle to detect the effects of air pollution on its lichen flora.

Methods

The impact of air pollution can be detected by sampling the lichen flora on similar substrates throughout the study area. The substrate selected was the bark of *Acer macrophyllum* Pursh. The bark texture of this tree is such that it is capable of supporting a diverse lichen flora when uninhibited by air pollution. The tree also occurs throughout the city of Seattle. Site selection was determined by the presence of ten exposed trees that were free of scars or other growth irregularities on the two meters above soil level.* The lower two meters of the trunks were sampled for species present. The percent cover for each species was recorded as well, using a modification of a Braun-Blanquet scale of cover abundance where + = 1-5 percent, 2 = 5-15 percent, 3 = 15-25 percent, 4 = 25-50 percent, 5 = 50-75 percent, and 6 = 75-100 percent (Stringer and Stringer, 1974). The air pollution factor of each site was then determined using the Index of Atmospheric Purity method developed by LeBlanc and DeSloover (1970).

The Index of Atmospheric Purity (IAP) is determined in the following manner: $IAP = \Sigma \frac{(Q \cdot F)}{10}$. F = the sum of the cover abundance values for each species and Q = the association index for each species. A 'Q' value for each species was derived by adding together the number of species that occur with it at a site and then taking the mean of the sums for all the sites where that species was present. This value gives weight to species that occur rarely yet are found in association with many other species. Those species that are weighted heavily would be the ones with a low level of tolerance to air pollution. Using this method, an IAP value is calculated for each site and plotted on a map. From this map the study area is arbitrarily subdivided into zones on the basis of range of IAP values.

The lichens found at the various sites were identified with the aid of keys prepared by Howard (1950) and Hale (1969). Nomenclature is according to Hale and Culberson (1970).

Description of Study Area

The study area is bounded by the city limits of Seattle, Washington. The city is constricted on both the western and eastern sides by large bodies of water. The annual precipitation is about 100 cm, most of which falls in the form of rain during the winter. The prevailing winds are from a southerly direction. The topography of the area has been determined largely by a combination of glacial erosion and deposition, which has resulted in the formation of numerous hills throughout the city extending in a north-south direction.

*At a few sites less than ten trees were sampled. These sites were included because of their strategic locations, and their values were weighted to appear as standard sites.

Results

Eighty-five sites were sampled throughout the city. Nineteen corticolous lichen species were recorded (Table 1). Five of the species were of the crustose type, three were fruticose, and eleven foliose.

TABLE 1. Distribution for the 19 lichen species present within the study area. For each species the percentage presence and mean coverage (based on the 1-5 scale of cover abundance) is shown for each IAP zone where a species is present. Percentage presence precedes the mean coverage value in each column.

Species	IAP Zone I	II	III	IV	V
Candelaria concolor	23/.013	19/.046	40/.149	40/.246	60/.220
Physconia grisea	30/.026	43/.053	83/.352	85/.593	100/.560
Cladonia balfourii	23/.046	43/.146	63/.388	85/.678	100/1.10
Caladonia chlorophaea	30/.040	50/.286	56/.331	67/.572	100/.680
Hypogymnia physodes	76/.16	100/.533	100/1.13	100/1.37	100/.294
Parmelia sulcata	46/.087	56/.293	83/.874	95/1.37	100/1.96
Xanthoria candelaria	8/.006		10/.028	28/.035	40/.160
Ochrolechia pallescens	8/.040	37/.227	37/.235	24/.075	20/.060
Lecidea scalaris	23/.060	43/.267	50/.481	67/1.05	100/.960
Lecanora hagnei		6/.006	26/.073	56/.236	60/.240
Hypogymnia tubulosa		19/.053	40/.206	38/.341	100/.520
Parmelia perlata		37/.047	50/.178	43/.341	60/.941
Parmeliopsis ambigua		19/.033	33/.141	48/.281	80/.760
Cladonia bellidiflora			3/.008	14/.120	60/.340
Unsea hirta			26/.012	28/.010	80/.020
Mycoblastus sanguinarius			3/.004	14/.080	
Ramalina farinacea			10/.004	19/.081	
Evernia prunastri				5/.015	
Caloplaca pyracea				10/.010	
Mean total coverage per tree	.053	.166	.269	.391	.764
% increase over previous zone		313	162	145	195

Discontinuities between the IAP values were used to subdivide the study area into five zones. Zone I includes all the sites with IAP values from 0-9, Zone II with IAP = 10-19, Zone III with IAP = 20-40, Zone IV with IAP = 41-69, and Zone V with IAP values greater than 69. The zones are not arranged in concentric circles about the city's center, but they do reflect a transitional gradient away from the pollution sources.

All species were found to increase in their mean percent coverage from Zones I-V, with the exception of *Lecidea scalaris* and *Ochrolechia pallescens*. These crustose species reached their peaks in Zones IV and II, respectively (Table 1). Although *Lecidea scalaris* reached its percent coverage peak in Zone IV, it was found at only 67 percent of the sites within that zone; in Zone V it was present at all of the sites but at lower cover values.

In Zone I nine lichen taxa were present at thirteen sites. Zone II contained twelve taxa at seventeen sites, Zone III held seventeen taxa at twenty-nine sites, Zone IV nineteen taxa at twenty-one sites, and Zone V contained fifteen taxa on five sites. Thus, there is an increase in species richness from Zone I to IV. The decrease in Zone V is most likely due to the low number of sites with high IAP values and the dominance of a few species at those sites.

Discussion

Although the IAP values do not form concentric circles which form a gradient of atmospheric purity, they do reflect land use patterns. Zone I corresponds to the central business district of the city and the area to the south that supports heavy industry (Fig. 1). This industrial area lies within a broad valley which is bordered on its eastern and

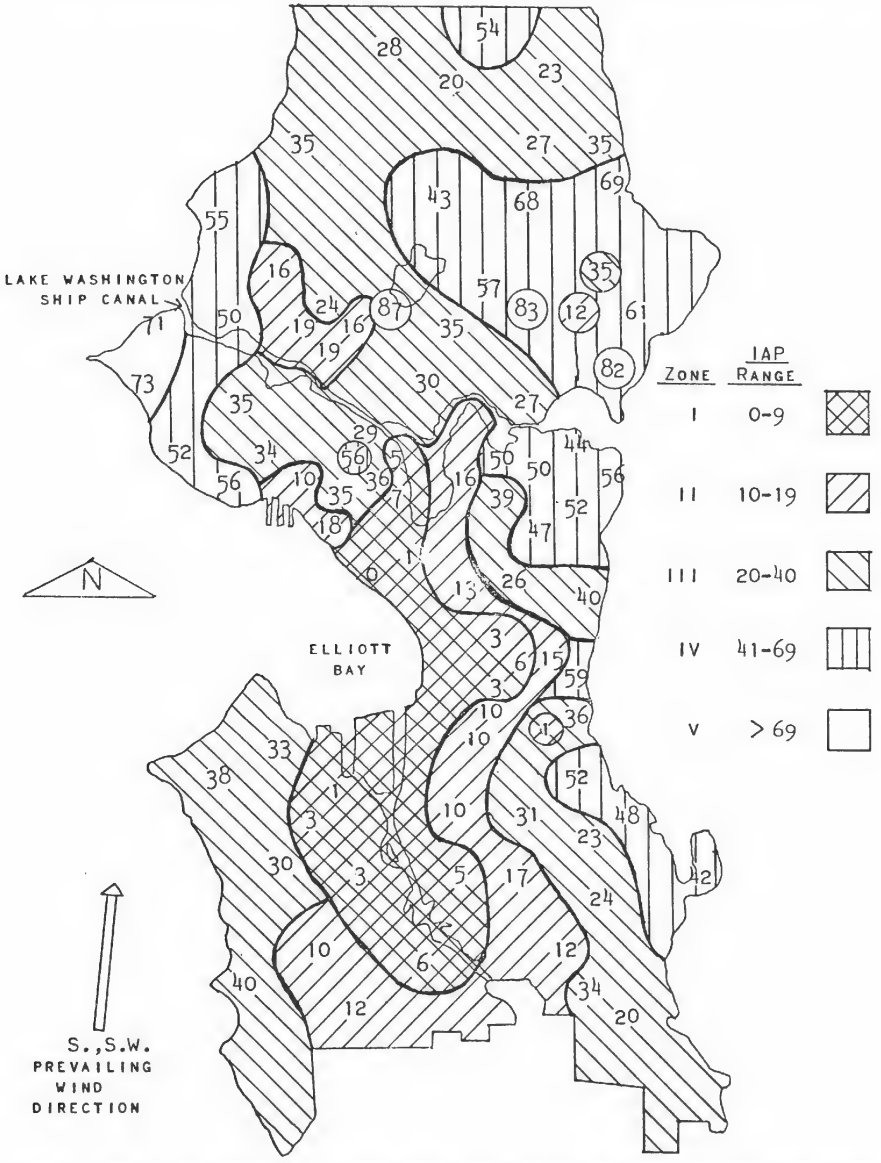

Figure 1. Map of the Seattle, Washington, study area showing the zones delimited on the basis of Index of Atmospheric Purity Values.

western sides by hills that are approximately 200 m high and extend in a southerly direction away from Elliott Bay. This topography acts to inhibit the dispersion of atmospheric pollutants. The single IAP value of one that occurs outside Zone I can be accounted for by the presence of heavy traffic patterns nearby. The lichen flora within this zone is extremely poor; the nine species present average far less than 1 percent coverage (Table 1).

Zone II occurs within three areas of the city. Its major portion flanks the eastern and southern portions of Zone I. The portion of the zone that runs north-south roughly corresponds to the crests of two major hills which separate the southern portion of the city. Since the prevailing winds in Seattle are southerly these hills may aid in channeling the atmospheric pollutants northward and act as a barrier to dispersion eastward. This hypothesis is reinforced by the fact that the IAP values between this portion of Zone II and neighboring Zone III show a very sharp boundary. The land use within Zone II is dense residential and small business.

The second portion of Zone II lies at the north end of Elliott Bay. This is an area of heavy industry that faces Elliott Bay. Prevailing winds from the south act to increase the dispersion rate and prevent the accumulation of pollutants that is observed within Zone I. The third portion of Zone II lies to the north with its southern boundary along the Lake Washington Ship Canal. Adjacent to the canal are water oriented industrial operations. The pollutants discharged into the air by these industries are apparently being carried northward by the prevailing winds. Although the land use of this area is to a large degree residential, there is a fairly large business district present which may be a contributing factor.

The lichen flora of Zone II is represented by twelve species. The species coverage averages three times that of Zone I but it is still less than 1 percent. This zone is best described as one of transition between severely polluted portions of the city and the most frequent condition which is represented by Zone III.

Zone III occupies the greater portion of the city and is almost entirely residential with scattered retail business districts. The lichen flora of this zone is most likely determined by the topography's effect on wind currents. The topography and increased temperature of a city act together to create wind turbulence that can cause ground level concentrations of pollutants to vary rapidly both temporally and geographically. Thus, peak concentrations of atmospheric pollutants become more difficult to predict as the distance from the source increases.

The lichen flora of this zone is represented by seventeen species with *Hypogymnia physodes* averaging a coverage of slightly greater than 1 percent and *Parmelia sulcata* approaching 1 percent.

Zone IV occupies the outlying portions of the city: they are almost totally residential and removed from the pollution sources. The areas of Zone IV in the southeast and the east central portion of the city both lie in the lee side of hills which can act as a barrier to pollution. The large area of Zone IV in the northeast portion of the city contains areas which belong in three other zones. The IAP values of 12 and 35 may be explained by their location on the southwest face of a hill near the crest. This exposure could allow for greater concentrations of air pollution than would be expected. The IAP value of 83 can be explained by its location on the lee side of a hill. The IAP value of 82 to the southeast occurs midway up the southwest face of an adjoin-

ing hill where it is exposed to southerly winds. There is no apparent explanation for this occurrence.

The lichen flora of Zone IV contains three species that occur with a frequency of greater than 1 percent (Table 1). There are two more species present in this zone than in the previous zone. These two additions occur in very small amounts and are found only within this zone. Therefore, the major difference between Zones III and IV is that Zone IV shows an increase in percent cover with the same species being present. The coverage is increased by about 165 percent between the two zones.

Zone V represents the least affected portion of Seattle's lichen flora. Although fewer species are found within this zone than in Zone IV (15 vs. 19), those that are present occur with relatively high coverage values; the total coverage is 200 percent greater than that in Zone IV. That portion of the zone located in the northwest part of the city is not in the direct path of atmospheric pollutants carried by the prevailing winds from the city's center, which alone can account for the observed diversity of the lichen flora.

The results of this study may be correlated with the sulfur dioxide data published by the Puget Sound Air Pollution Control Agency (1975). Their data are obtained through the use of sensitive monitoring devices that are located at three points within the city. Table 2 shows the sulfur dioxide concentrations measured and the IAP zone in which the monitors are located. It is not really of any value to attempt to compare the results of this study with those found in studies of a similar nature in different cities because climatic variations between cities are such that their lichen floras can be extremely variable (Hawksworth, 1973).

TABLE 2. Puget Sound Air Pollution Control Agency sulfur dioxide data for Seattle, Washington, and the IAP zones in which the three monitoring devices were located.

IAP Zone	annual mean	highest 24 hr. mean	highest 1 hr. mean
III	8.0 ug/m^3	79.8 ug/m^3	266.0 ug/m^3
I	16.0 ug/m^3	159.6 ug/m^3	558.6 ug/m^3
I	23.9 ug/m^3	159.6 ug/m^3	771.3 ug/m^3

On the basis of percent cover and frequency of occurrence, the most tolerant species were found to be *Hypogymnia physodes*, *Parmelia sulcata*, *Physconia grisea*, *Lecidea scalaris*, and *Candelaria concolor*. The species *Hypogymnia physodes* is one of the most common and tolerant lichen species known. Tallis (1964) has placed its threshold level of tolerance at 140 ug/m^3, which correlates well with its limited distribution in Zone I where the Puget Sound Air Pollution Control Board has determined a peak average sulfur dioxide concentration of 160 ug/m^3 for a twenty-four hour period. *Parmelia sulcata* and the other four species are all known to occur at sulfur dioxide concentrations of about 70 ug/m^3 (Ferry, Baddeley, and Hawksworth, 1973). *Parmelia perlata* and *Parmeliopsis ambigua* are both excluded from Zone I and occur with very low values in Zone II. In other studies of this nature, they have been found at sulfur dioxide concentrations of 35 ug/m^3 and 60 ug/m^3, respectively (Ferry, Baddeley, and Hawksworth, 1973). These values are less than those applied to Zone III from the Puget Sound Air Pollution Control Board data.

Conclusion

This study has established a good correlation between air pollution and the distribution of corticolous lichens for the city of Seattle. The major factor affecting that distribution appears to be the topography of the city and its influences on the movement of prevailing winds at ground level. The topography of the city acts as a barrier to pollution dispersion in some areas and as a channeling device in others. In comparing the lichen flora of Seattle with that of many European cities in which such studies have been conducted, it is observed that Seattle lacks the central lichen desert that is found in most cities. This fact may be attributed to our laws governing pollution emissions, or it may be due to the weather patterns which prevent concentrations from building up in toxic quantities. Seattle also is exceptional in that it has cheap electrical energy available that is generated without the pollution that accompanies fossil fuel generating plants.

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Parasitic Mites of the Mountain Beaver (Aplodontia rufa) from Oregon[2]

Abstract

Two laelapid, *Alphalaelaps aplodontiae* and *Patrinyssus hubbardi*, and one listrophorid, *Aplodontochirus borealis*, constituted the major parasitic mite fauna on mountain beavers (*Aplondontia rufa*) in Oregon.

Introduction

Previous records of ectoparasitic mites of the mountain beaver (*Aplodontia rufa*) were summarized by Whitaker and Wilson (1974), but there is no general paper on mountain beaver ectoparasites. The purpose of this paper, therefore, is to present data on the ectoparasitic mites found in the fur of the mountain beaver from Oregon.

Methods and Materials

Forty mountain beavers, trapped along the Oregon coast from 1970 through 1972, were studied. They were placed in white porcelain pans and those mites that left a carcass and crawled about on the pan were collected initially. Additional mites were brushed from the fur with a fine, stiffly bristled toothbrush; finally, the fur of each animal was examined with the aid of a 16-power hand-lens.

In contrast, eight mountain beavers from Clackamas County, Oregon, were not examined with the aid of a hand-lens, although the fur was closely examined with a teasing needle. These animals were placed in tin cans, from whose inner sides the vast majority of the mites were collected as they left the carcasses. The cans containing the

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carcasses were refrigerated for several days between sessions of mite removal. Some of the mountain beavers were additionally washed in a detergent solution.

Mites were preserved in 70 percent ethanol, cleared and stained in Nesbitt's solution containing acid fuchsin, and mounted in Hoyer's solution; cover slips were ringed with Euparal.

Description of Study Area

Mountain beavers trapped along the Oregon coast were from the Coast Range and Klamath Mountains physiographic provinces, whereas those from Clackamas County were in the Western Cascades physiographic province (Franklin and Dyrness, 1973). Within these physiographic provinces, the mountain beavers inhabited the Sitka Spruce (*Picea sitchensis*) and Western Hemlock (*Tsuga heterophylla*) Zones (Franklin and Dyrness, 1973).

Along the Oregon coast, mountain beavers primarily occupy the Alder/Salmonberry (*Alnus rubra/Rubus spectabilis*) habitat which, with rare exception, is an early seral community (Maser and Franklin, 1974). Mountain beavers are in fact predominantly early to mid seral-stage animals throughout their geographical range (Scheffer, 1929).

Results and Discussion

All forty-eight mountain beavers examined had mites (Table 1). Seven species of mites were found along with unidentified *Euryparasitus* sp. (probably more than one species involved).

TABLE 1. Mites found in the fur of 48 mountain beaver, **Aplodontia rufa,** from Oregon.

	Hosts infested		No. of mites	
	No.	%	Total	x
Laelapidae				
Alphalaelaps aplodontiae	45	97.8	1009	21.0
Patrinyssus hubbardi	25	52.1	422	8.8
Haemogamasus reidi	1	2.1	11	0.3
Haemogamasus sp. (apparently a new species)	4	8.3	24	0.5
Listrophoridae				
Aplodontochirus borealis*	3	37.5	210	26.25
Glycyphagidae				
Microlabidopus americanus*	1	12.5	40	5.0
Aplodontopus latus*	1	12.5	2	0.25
Cyrtolaelapidae				
Euryparasitus sp.	2	4.2	4	0.1

*figured on the basis of the 8 individuals examined by Wallace.

Two large forms of mites were common, *Alphalaelaps aplodontiae* and *Patrinyssus hubbardi.* Although we have taken a few individual mites of these species from other western Oregon mammals (unpub. data), both species are basically host-specific to mountain beavers.

Alphalaelaps aplodontiae moves rapidly and readily abandons a mountain beaver carcass when it is disturbed. In fact, one of us (Wallace) had this species of mite climb onto and bite him. This species often clustered around the genitalia and the base of the tail of a host.

Three species of tiny mites were found: *Aplodontochirus borealis* (Listrophoridae).

Microlabidopus americanus, and *Aplodontopus latus* (both Glycyphagidae). These species were found only on the eight mountain beavers from Clackamas County, probably a reflection of the collecting methods. We suspect these three tiny forms, known only from mountain beavers, to be much more abundant than our data indicate. A few specimens of *Haemogamasus* sp., apparently a new species, were also taken and are currently under study.

Although we found *Haemogamasus reidi* on one mountain beaver, this mite is primarily associated with squirrels, whereas *Euryparasitus* sp. has been found on a number of species of mammals in Oregon and elsewhere (unpub. data).

Alphalaelaps aplodontiae, *Aplodontopus latus*, and *Microlabidopus americanus* have been previously taken from mountain beaver in Oregon, but *Patrinyssus hubbardi* and *Aplodontochirus borealis* had been known only from Washington.

Summary and Conclusion

According to Shotwell (1958), the mountain beaver (*Aplodontia rufa*)—often referred to as a "living fossil"—has lived in similar habitat and correspondingly has exhibited only minor morphological changes since the late Miocene. They did move with their environment, however, which was sharply compressed westward by topographic changes in the Cascade Mountains and subsequent regional climatic change.

Mountain beavers have long been rather sedentary, fossorial rodents that construct extensive burrow systems (Johnson, 1971; Martin, 1971; Voth, 1968), thus creating a stable environment. It is not surprising, therefore, that five of the six mites identified to species are host-specific to the sole surviving member of an ancient rodent family, since long-term isolation should lead to a host-specific mite community if the mites are unable to complete their life cycles on alternate hosts with different habits and habitats.

But this finding does not rule out the fact that *Alphalaelaps aplodontiae* and *Partrinyssus hubbardi* have been occasionally found on other species of western Oregon mammals, and that *Haemogamasus reidi* is primarily associated with squirrels. One of us (Maser) has trapped the following mammals in mountain beaver burrows: shrew-moles (*Neurotrichus gibbsi*), coast moles (*Scapanus orarius*), snowshoe hares (*Lepus americanus*), brush rabbits (*Sylvilagus bachmani*), Townsend chipmunks (*Eutamias townsendi*), deer mice (*Peromyscus maniculatus*), California red-backed voles (*Clethrionomys californicus*), Oregon voles (*Microtus oregoni*), Pacific jumping mice (*Zapus trinotatus*), long-tailed weasels (*Mustela frenata*), short-tailed weasels (*M. erminea*), mink (*M. vison*), and spotted skunks (*Spilogale putorius*). Wallace also caught a short-tailed weasel in a mountain beaver burrow in Clackamas County. In addition, mountain beavers are preyed upon by such animals as the bobcat (*Lynx rufus*) (Nussbaum and Maser, 1975). Under such circumstances, some interspecific mite transfer would be expected.

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Food and Ectoparasitic Mites of Oregon Moles[2]

Abstract

The major food in stomach samples of Oregon coast moles (*Scapanus orarius*), Townsend moles (*S. townsendi*), and shrew-moles (*Neurotrichus gibbsi*) was earthworms. Other important foods were adult and larval insects, centipedes, molluscs, and vegetation. The more abundant mites found in the fur were *Euryparasitus* sp. and *Haemogamasus occidentalis* on all three species of moles, and *Haemogamasus reidi*, *Pygmephorus* sp., and *Eulaelaps stabularis* on Townsend moles.

Introduction

There is a paucity of information on food habits and parasitic mites of western North American moles, *Scapanus* and *Neurotrichus*. The purpose of this paper is to extend existing knowledge and to present new information on food habits and fur mites of these moles.

Methods and Materials

Moles collected from 1961 through 1963 were taken in Tillamook County near the coast, whereas those trapped from 1970 through 1972 came from the following locations: (1) shrew-moles and coast moles were trapped along the coast in Curry, Coos, Douglas, Lane, and Lincoln Counties; (2) most of the Townsend moles were trapped in the same areas, but a few were collected in Benton County in the Willamette Valley; (3) the broad-footed mole (*Scapanus latimanus*) was taken near the California border in Klamath County.

Stomach contents of 182 Townsend moles caught from 1961 through 1963 had wet

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weights recorded prior to the identification of the contents. Stomach contents of the 182 moles examined by Pedersen are reported separately because they were not analyzed in as much detail as were those in Table 1. Stomach contents of moles that were trapped from 1970 through 1973 were preserved, without being weighed, in 10 percent formalin. The contents were identified and the percent volume by food type in each stomach was visually estimated using a 10 to 70 power zoom dissecting microscope.

Mites collected from all moles were preserved in 70 percent ethanol, cleared and stained in Nesbitt's solution containing acid fuchsin, and mounted in Hoyer's solution; cover slips were ringed with Euparal. When necessary, identity of representative specimens of mites was verified by specialists.

TABLE 1. Food of moles from Oregon.

Number examined	**Neurotrichus gibbsi** 11		**Scapanus orarius** 25		**Scapanus townsendi*** 28	
	% vol	% freq	% vol	% freq	% vol	% freq
Earthworms (Annelida)	48.5	81.8	56.2	92.0	54.9	92.9
Centipedes (Chilopoda)	4.3	54.5	6.3	48.0	1.4	32.1
Millipedes (Diplopoda)			0.4	8.0		
Snails & Slugs (Mollusca)	4.1	9.1	1.7	28.0	1.6	17.9
Spider (Araneida)			0.6	4.0	trace	3.6
Mite (Acarina)						
Insect larvae						
Lepidoptera			1.2	12.0	0.5	14.3
Tipulidae (Diptera)	7.5	9.1	0.6	4.0	2.1	14.3
Unidentified Diptera	2.4	36.4	1.5	16.0	4.9	14.3
Scarabaeidae (Coleoptera)			0.6	8.0		
Carabidae (Coleoptera)			0.2	8.0	0.3	7.1
Elateridae (Coleoptera)			1.0	12.0		
Unidentified Coleoptera	10.0	27.2	1.0	20.0	2.9	35.7
Unidentified insects			1.3	2.4		
Pupae						
Formicidae (Hymenoptera)			3.9	20.0	0.1	7.1
Earthworm (Annelida)					0.1	3.6
Unidentified pupae			1.3	16.0		
Insect Adult						
Scarabaeidae (Coleoptera)			1.7	16.0		
Chrysomelidae (Coleoptera)			0.2	4.0	0.2	3.6
Chauliognathus (Coleoptera)			0.3	8.0		
Unidentified Coleoptera	1.4	18.2	0.1	4.0	0.4	10.7
Formicidae (Hymenoptera)			6.1	44.0	0.3	10.7
Halictidae (Hymenoptera)					0.2	3.6
Unidentified Hymenoptera			0.2	4.0		
Gryllidae (Orthoptera)					0.1	3.6
Unidentified insects	3.6	18.2	0.1	4.0	0.8	21.4
Insect internal organs	10.0	18.2				
Mammal						
Shrew or mouse remains			6.0	8.0	2.1	7.1
Vegetation						
Endogonaceae (fungus)			0.4	12.0		
Unidentified fungi			trace	4.0		
Seeds			2.0	4.0	6.8	10.7
Clover flowers					0.1	3.6
Moss					0.2	3.6
Unidentified vegetation	0.6	18.2	1.9	28.0	9.1	53.6
Unidentified material	7.7	18.2	3.5	16.0	11.0	42.9
	100.1		100.3		100.1	

*Only the 28 **Scapanus townsendi** that were trapped from 1970 through 1973 have been included in this table.

Description of Study Area

Moles, with the exception of the single broad-footed mole, were trapped in the Coast Range and Willamette Valley physiographic provinces as described by Franklin and Dyrness (1973). The broad-footed mole was collected in the Basin and Range physiographic province (Franklin and Dyrness, 1973).

Townsend moles and shrew-moles occur throughout most of western Oregon in the following major vegetational zones as defined by Franklin and Dyrness (1973): (1) Sitka Spruce (*Picea sitchensis*) Zone, (2) Western Hemlock (*Tsuga heterophylla*) Zone, (3) Willamette Valley, (4) Umpqua and Rogue Valleys, and (5) Mixed Conifer and Mixed Evergreen Zones.

Coast moles occur throughout western, extreme west-central, and northeastern Oregon in all vegetational zones.

Broad-footed moles inhabit the eastern flank of the Cascade Mountain Range from mid-state southward through south-central Oregon into California (Bailey, 1936). The single specimen was trapped in the shrub-steppe (with big sagebrush, *Artemisia tridentata*) Zone (Franklin and Dyrness, 1973).

Results and Discussion

Food

Stomach contents were examined from four species of moles: 11 shrew-moles, 25 coast moles, 28 Townsend moles, and a broad-footed mole. The stomach of the broad-footed mole, allopatric to the other species, contained 80 percent molluscs and 20 percent unidentified Coleoptera. Data for the other three species are summarized in Table 1.

Except for the broad-footed mole, earthworms were the most important food item for moles in this study. Wight (1928) found nearly 75 percent of the food in 306 Townsend mole stomachs to be earthworms, whereas Moore (1933) found earthworms to comprise 69.9 percent of the contents of 8 coast mole stomachs and 76.1 percent of 42 Townsend mole stomachs. Dalquist and Orcutt (1942) found earthworms to comprise 42 percent of the stomach contents of 39 shrew moles. Earthworms are also frequently the major food item in the diets of eastern moles—the star-nosed mole (*Condylura cristata*) (Hamilton, 1931) and the eastern mole (*Scalopus aquaticus*) (Whitaker and Schmeltz, 1974).

Moles occasionally feed on vegetation (Dalquest and Orcutt, 1948; Silver and Moore, 1941): vegetation represented 15.9 percent of the stomach contents of Townsend moles and 1.2 percent of the stomach contents of coast moles (Moore, 1933). All moles in this study, except the broad-footed mole, fed on some vegetation (Table 1).

The shrew-mole is active on the surface and also is a shallow burrower in the humus of western Oregon forests and the surface soils of meadows. They also spend much time around rotten logs on the forest floor, which probably accounts for the high frequency (54.5 percent) of centipedes in their diet. This species commonly captures large insects and eats only the internal organs, which comprised 10 percent of the volume. Other important foods were coleopteran and tipulid larvae and molluscs. Maser and Franklin (1974) identified the centipede (*Scolopocryptos sexpinosa*), pill bugs (*Armadillidum vulgare*), sow bugs (*Porcellio scaber*), and termites as food items of shrew-moles. In addition, Dalquest and Orcutt (1942) identified isopods, various unidentified insect larvae and pupae, and springtails as food items of shrew-moles in Washington. Since

it is the smallest mole in North America, size and durability of prey are probably limiting factors in the variety of food items this mole can use: note, for example, the relative absence of beetles with hard elytra in its diet (Table 1).

Coast moles, geographically the most wide-ranging species in Oregon, show a correspondingly varied diet (Table 1). Primarily inhabitants of western coniferous forests, these moles tend to be shallow burrowers in both forests and forest/meadow ecotones. They also are active on the surface of the forest floor, especially around large rotten logs. Their wide latitude in habitat use allows them to exploit a great diversity of food items.

Townsend moles, the largest of the western moles, are primarily inhabitants of meadows and pastures, a more limited habitat than that enjoyed by the other two species, and which appears to impose some restrictions on the variety of food items available (Table 1). This point is further illustrated by food-habit data collected on Townsend moles by one of us (Pedersen) from 1961 through 1963. Stomachs of 182 Townsend moles trapped in Tillamook County pasturelands contained two major food items—earthworms and roots from pasture grasses.

Stomach contents of 106 males averaged 63.7 percent earthworms by volume; those of 76 females averaged 65.8 percent. The weight of earthworms in 79 percent of the stomachs ranged from 200 mgs to 4000 mgs. The largest amount of earthworms found in a single stomach was 9700 mgs.

Stomach contents of 106 males averaged 36.3 percent grass roots, whereas those of 76 females averaged 39.2 percent roots. The highest weight of grass roots found in a single stomach was 3870 mgs. "Root balls" were found in 36 stomachs. The root balls were cylindrical, 10 mm x 5 mm, dark brown, and compacted. Neither the cause nor the function of these root balls is known. In contrast, only six stomachs contained traces of insect exoskeletons, and one stomach contained 100 percent mollusca (slugs).

Differences in habitat orientation, depth of burrowing, and size of shrew-moles, coast moles, and Townsend moles suggest a partitioning of the available food resources (Table 1) which should tend to decrease interspecific competition for food where these species are sympatric.

Mites

Mites were found on shrew-moles, coast moles, and Townsend moles, but no mites were found on the single broad-footed mole (Table 2). The more abundant mites on moles of Oregon were *Haemogamasus occidentalis* and *Euryparasitus* sp., both of which were found on all three species. *Haemogamasus reidi* and *Pygmephorus* sp. were found on four Townsend moles and *Eulaelaps stabularis* on three. Otherwise no species of mite was found on more than two moles of any one species. The myobiid mite, *Eadiea scapanus*, was found during the present study and described as new (Fain and Whitaker, 1975). *Androlaelaps fahrenholzi*, a very common and widespread species, was found on two coast and two Townsend moles. The mites from coast moles, listed as *Hirstionyssus obsoletus?* (variant), are undergoing further study, but have been found on several species of Oregon mammals.

Mites previously reported from shrew-moles, but not found during the present study, were *Haemogamasus keegani*, *H. liponyssoides*, and *Hirstionyssus utahensis*. Those previously found on Townsend moles but not found during the present study were

Haemogamasus ambulans and *Hirstionyssus obsoletus.* Only *Haemogamasus occidentalis* had been previously reported from coast moles.

TABLE 2. Mites of the fur of moles from Oregon.

	Neurotrichus gibbsi				**Scapanus orarius**				**Scapanus townsendi**			
	No. mites		Hosts parasitized		No. mites		Hosts parasitized		No. mites		Hosts parasitized	
	Total	x	No.	%	Total	x	No.	%	Total	x	No.	%
No. examined	(26)				(16)				(24)			
					Parasitic Forms							
Laelapidae												
Haemogamasus occidentalis	13	0.50	8	30.8	114	7.13	15	93.8	167	6.96	18	75.0
H. reidi	—	—	—	—	1	0.06	1	6.3	13	0.54	4	16.7
H. ambulans	—	—	—	—	1	0.06	1	6.3	—	—	—	—
Androlaelaps fahrenholzi	—	—	—	—	6	0.38	2	12.5	12	0.50	2	8.3
A. casalis	—	—	—	—	1	0.06	1	6.3	—	—	—	—
Eulaelaps stabularis	—	—	—	—	2	0.13	2	12.5	4	0.17	3	12.5
Hirstionsyssus obsoletus (variant)	—	—	—	—	7	0.44	1	6.3	—	—	—	—
Laelaps kochi	1	0.04	1	3.8	—	—	—	—	—	—	—	—
Myobiidae												
Eadiea scapanus	—	—	—	—	—	—	—	—	23	0.96	2	8.3
E. brevihamata	9	0.35	1	3.8	—	—	—	—	—	—	—	—
Eutalpacarus peltatus	5	0.19	2	7.6	—	—	—	—	—	—	—	—
Protomyobia brevisetosa	—	—	—	—	—	—	—	—	1	0.04	1	4.2
Glycyphagidae												
Glycyphagus hypudaei	—	—	—	—	—	—	—	—	1	0.04	1	4.2
Listophoridae												
Listrophorus mexicanus	—	—	—	—	—	—	—	—	1	0.04	1	4.2
Pygmephoridae (**Pygmephorus** is probably parasitic)												
Pygmephorus horridus	—	—	—	—	1	0.06	1	6.3	—	—	—	—
Pygmephorus sp.	1	0.04	1	3.8	1	0.06	1	6.3	5	0.21	4	16.7
Bakerdania sp.	11	0.42	2	7.6	—	—	—	—	8	0.33	2	8.3
					Non-parasitic Forms							
Cyrtolaelapidae												
Euryparasitus sp.	9	0.35	4	15.4	3	0.19	2	12.5	8	0.33	8	33.3
Ascidae												
Proctolaelaps sp.	—	—	—	—	—	—	—	—	7	0.29	2	8.3
Pseudoparasitus sp.	3	0.12	1	3.8	—	—	—	—	—	—	—	—

New host records for mite species (see Whitaker and Wilson, 1974) are as follows: (1) shrew-moles—*Laelaps kochi* and *Eadiea brevihamata*, (2) coast moles—*Haemogamasus ambulans*, *H. reidi*, *Androlaelaps fahrenholzi*, *A. casalis*, *Eulaelaps stabularis*, *Hirstionyssus obsoletus*, and *Pygmephorus horridus*, and (3) Townsend moles—*Haemogamasus reidi*, *H. keegani*, *Eulaelaps stabularis*, *Protomyobia brevisetosa*, and *Glycyphagus hypudaei.* Above mites not previously reported from Oregon are *Protomyobia brevisetosa*, *Eutalpacarus peltatus*, *Eadiea brevihamata*, and *Glycyphagus hypudaei.*

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Some Foliage Nutrient Levels in Tree and Brush Species Growing on Pumice Soils in Central Oregon[1]

Abstract

Foliar analysis is becoming an important tool in evaluating soil fertility and site quality. During soil-vegetation studies on pumice soils in Central Oregon, foliage samples from six tree species and four shrub species were collected from five sites and analyzed for major and minor nutrient elements. There were marked differences in nutrient levels between species, but none were observed between sites. Tree foliage levels of the nutrients for which analyses were made indicated adequate supplies of everything but sulfur.

Introduction

In several fields of research including plant nutrition, plant ecology, soil fertility and even mineral prospecting, plant foliage analyses have come to play an important role in recent years (Beadle, 1954; Everard, 1973; Malyuga, 1964; Stone, 1968). They are used for the assessment of the nutrient status of plants and soils including the detections of deficiencies and toxicities. Some plants that accumulate metallic elements in particular have become useful means of finding mineral deposits.

Following field responses in ponderosa pine to additions of a sulfur fertilizer, a bioassay was recently made of the amounts of plant-available sulfur in the different layers of volcanic pumice ash present at five sites in central Oregon (Will and Youngberg, 1977). At the time soil samples were being collected, foliage samples were taken from the tree and brush species present.

Methods

Field Sampling

Foliage samples were collected from the five sites—Century Drive (CD), Royce Mt. (RM), Walker Rim (WR), Antelope unit (AU) and China Hat Mt. (CH) in mid-August 1971. Descriptions of these sites have been reported (Chichester *et al.*, 1969). Microsite differences on the sample sites were negligible. Sites were level to gently sloping and horizon thickness and depth to the paleosole were uniform for each site.

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The productivity of the Royce Mt. site is somewhat higher and that of the China Hat site somewhat lower than the other three sites due to higher total precipitation and coarser pumice, respectively.

Ponderosa pine (*Pinus ponderosa* Dougl.), lodgepole pine (*Pinus contorta* Dougl.), white pine (*Pinus monticola* Dougl. ex D. Don), grand fir (*Abies grandis* [Dougl.] Lindl.), silver fir (*Abies amabilis* [Dougl.] Forbes), and hemlock (*Tsuga mertensiana* [Bong.] Carr) were sampled by locating unsuppressed trees up to 10 m in height and clipping current season's shoots from a point 1 to 3 m from the top of each tree. At least 10 trees of each species were sampled at each site to give representative composite samples.

Full size leaves from current season's shoots were collected from snowbrush (*Ceanothus velutinus* Dougl.), manzanita (*Arctostaphylos patula* Greene) and chinquapin (*Castanopsis sempervirens* [Kell] Dudl.), while whole lengths of current shoots were taken from bitterbrush (*Purshia tridentata* [Pursh] DC.). For these brush species composite samples were collected from 15-20 plants at each site. All samples were dried at 60°-70°C before grinding; one composite sample of each species for each site was analyzed.

Chemical Analyses

After dry ashing oven dried samples, an HCl extract of the ash was analyzed as follows: P by colorimetric determination with molybdovanadate and K, Ca, Mg, Zn, Fe, and Mn by atomic absorption. Boron was determined colorimetrically in an ash extract using carmimic acid. X-ray fluorescence was used to determine S in the ground material.

Results and Discussion

The results of analyses are given in Table 1. Because this was not an exhaustive study, no detailed conclusions or long discussion are justified; but where species were present at four or five of the sites, consistent difference in nutrient concentrations almost certainly indicate differences between species:

1) Ponderosa, lodgepole, and white pines have consistently lower foliage levels of Ca and Mg than snowbrush, manzanita, and bitterbrush;

2) Lodgepole and white pine are higher in Mn content than ponderosa pine; and

3) Snowbrush tends to be high in Fe while manzanita and bitterbrush are low in Mn.

Although other species occurred at only one or two sites, the following marked differences are of interest:

1) The firs and hemlock are higher in Ca (but not Mg) than the pines; and

2) The firs, chinquapin, and particularly hemlock have very high Mn levels.

Leaf's (1968) review of the foliar K, Mg, and S levels in forest trees did not include the species reported in this paper. Comparisons with related species, however, indicate that in general, trees in Central Oregon have adequate K, low to adequate Mg, and deficient to low S. The latter agrees with a bioassay of available S in the soil (Will and Youngberg, 1977). The authors consider S levels 0.06 percent to be deficient. In reviewing the trace element contents of tree foliage, Stone (1968) included grand fir. Although the Mn content was in the high range of species in this study, it was well be-

low the 2272 ppm cited by Stone for grand fir. All the B, Zn, Fe, and Mn figures reported in this paper appear to indicate adequate levels of supply.

TABLE 1. Foliage nutrient concentrations in tree and brush species from five sites in central Oregon.

Species and Location		P	K	Ca	Mg	S	B	Zn	Fe	Mn
		%					ppm			
Ponderosa pine	CD	0.22	0.90	0.20	0.10	0.06	22	36	25	110
	AU	0.20	1.00	0.20	0.09	0.08	24	35	25	115
	WR	0.23	1.05	0.22	0.10	0.06	21	34	30	185
	RM	0.23	1.30	0.23	0.09	0.08	25	38	35	100
	CH	0.25	0.97	0.21	0.12	0.08	30	47	25	140
Lodgepole pine	AU	0.17	0.85	0.22	0.12	0.08	28	55	40	225
	WR	0.14	0.70	0.21	0.09	0.05	26	35	40	280
	RM	0.16	0.90	0.22	0.09	0.08	20	43	35	330
	CH	0.17	0.68	0.22	0.10	0.06	25	51	35	215
Snowbrush	CD	0.18	0.90	0.55	0.17	0.06	31	36	55	65
	AU	0.14	0.95	0.52	0.15	0.06	21	12	60	120
	WR	0.16	1.00	0.46	0.16	0.07	30	18	50	105
	RM	0.14	0.90	0.52	0.14	0.12	20	30	75	290
Manzanita	CD	0.18	1.00	0.40	0.23	0.06	13	45	30	40
	AU	0.19	1.00	0.40	0.19	—	14	33	35	80
	WR	0.20	1.10	0.41	0.16	—	16	32	35	45
	RM	0.20	1.10	0.38	0.14	0.08	19	40	50	35
Bitterbrush	CD	0.20	0.95	0.40	0.15	—	27	31	50	25
	AU	0.18	0.95	0.38	0.16	—	19	13	55	30
	CH	0.20	0.95	0.37	0.14	—	18	29	50	20
White pine	WR	0.21	1.10	0.23	0.11	—	22	32	35	230
	RM	0.20	1.10	0.24	0.10	0.09	30	45	45	240
Grand fir	RM	0.14	1.00	0.45	0.12	0.06	23	31	50	790
Silver fir	RM	0.18	1.05	0.43	0.12	0.06	26	33	40	825
Hemlock	RM	0.16	0.64	0.33	0.08	0.06	29	15	60	1780
Chinquapin	RM	0.13	0.70	0.38	0.12	0.09	39	16	60	740

Summary

No marked differences in foliar nutrient levels were observed between sites, but there were considerable species differences. The most noticeable of these were (1) high Ca and Mg in snowbrush, manzanita, and bitterbrush, and (2) the great variation in Mn levels between species—lodgepole and white pines having higher contents than ponderosa pine, but not nearly as high as the firs and hemlock. Manzanita and bitterbrush are very low in Mn. Tree foliage levels indicate adequate supplies of all nutrients except S.

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Movements and Home Range of the Porcupine in Northeastern Oregon

Abstract

Capture-recapture techniques and radio-telemetry were used in an investigation of porcupine (*Erethizon dorsatum*) movements and home range in a ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) forest in northeastern Oregon. Significantly ($p<0.05$) shorter movements in December to February as compared with April to July were related to seasonal changes in weather and vegetation. An average yearly home range size of 70.1 ha was found for two female porcupines radio-tracked from February through August. The maximum distance between recaptures was 525 m to 1156 m, which compares closely to the length of home range areas for porcupines radio-tracked during the study.

Introduction

Porcupines frequently cause extensive silvicultural damage resulting in severe losses in young timber stands. Consequently most studies of porcupines have dealt with appraising damage to trees and controlling porcupine numbers. Little research has been reported on movements and behavioral patterns. The porcupine occupies a wide geographical range and occurs in many different vegetation types. Probably movements and behavior vary with habitat. This report discusses movements and home range in a ponderosa pine and Douglas-fir forest in northeastern Oregon.

Study Area

Research was conducted on a 1500 ha area in the Heppner Ranger District of the Umatilla National Forest, located 60 km south of Heppner, Oregon. Detailed descriptions of the region can be found in Franklin and Dyrness (1973) and Hall (1973). The study site vegetation varied from sparsely scattered junipers (*Juniperus occidentalis*) with a bunchgrass (*Poa sandbergii*) ground cover to ponderosa pine and Douglas-fir stands with a groundcover of sedge (*Carex* sp.), strawberry (*Fragaria virginiana*), heartleaf arnica (*Arnica cordifolia*), pea (*Lathyrus* sp.), and snowberry (*Symphoricarpos albus*).

Methods and Materials

Field work was conducted from June 1973 through August 1974. Porcupines were captured in a 20-gal plastic garbage can, weighed, and immobilized with phencyclidine hydrochloride (Sernylan: Parke, Davis and Company) and triflupromazine hydrochloride (Vetame: E. R. Squibb and Sons) at a dosage level of one mg per kg of body weight (Seal and Erickson, 1969). After immobilization each animal was measured and its sex was determined. Age was calculated using the dental-age correlation established by Kochersberger (1950) and Dodge (1967), which is based on eruption, replacement, and wear patterns of the cheek teeth. Numbered, color-coded, plastic discs were attached to the ears using aluminum self-piercing domestic livestock eartags (Hasco style #1-

851, National Band and Tag Company, Newport, Kentucky).

Capture-recapture techniques and biotelemetry were used to study movements and home range. A vehicle was driven in the evening hours on a 7.6 km route throughout the summers of 1973 and 1974 for a total of 68 trips. Porcupines seen in the headlights were identified if previously captured, and processed if new animals. One hundred eighteen porcupines were captured one or more times during the study for a total of 231 captures.

An additional 32 porcupines were captured between December 1973 and August 1974 in a separate radio-tracking study area. Nineteen of these animals were observed two or more times for a total of 67 observations. Six porcupines were tagged with radio transmitters as described by Marshall *et al.* (1962) and were tracked intensively for a total of 495 animal-days. Tracking was from February through August 1974 and the number of tracking days per animal varied with capture date and telemetry capabilities. Fixes were plotted on tracing paper overlays from aerial photographs, and home range areas were measured using a portable area meter (model L1-3000, Lambda Instrument Corporation). Geometric centers of activity were determined using the method of Hayne (1949). Activity radii (Dice and Clark, 1953) were calculated from these geometric centers of activity. In this study all areas of porcupine activity were included within the home range boundaries. Feeding behavior was observed visually and was compared to feeding behavior reported in the literature.

Results and Discussion

Average distances for the move from one day's resting location to the next day's location are given in Table 1. Distances reported are for the linear distances between the locations and are not necessarily distance traveled by porcupines. Porcupines usually did not move in straight lines as observed by tracks in the snow, but in meandering routes which were often two or three times as long as the linear distance between successive resting locations. An analysis of variance (among months; df = 9, MS = 4936435.5; within months; df = 136, MS = 639147.4) is significant at the $p = 0.05$ level. Computation of the least significant difference shows that movements during December to February are different ($p<0.05$) from movements during April to July. Seasonal changes in weather and food availability appear to control the extent of porcupine movements. From August through February porcupines fed on the needles and the inner bark of trees. Rain and snow storms decreased movements as animals sought shelter either in trees or dens. Such was the case for January and February when individuals were ob-

TABLE 1. Average distances between daily resting locations for porcupines in northeastern Oregon.

Month	Number of observations	Distance in meters
November	1	181
December	8	100
January	15	34
February	10	80
March	4	234
April	12	328
May	25	442
June	38	360
July	3	370
August	30	246

served to remain in the same tree for as long as 16 days. Similar behavior was observed by Hoffer (1967) in a northern California pine-juniper forest and by Brander (1973) in a Michigan hardwood-hemlock forest. Porcupine movements gradually increased in the spring as the diet switched from bark and needles to succulent ground vegetation. Ground vegetation composed the bulk of the diet with the porcupines moving every night searching for favored foods until hot weather in July caused the vegetation to dry out. When this event occurred, porcupines gradually resumed feeding on tree needles and bark and their movements decreased.

Home range variables for six porcupines are given in Table 2. Areas vary greatly according to the method used to calculate home range size. The minimum area method (Mohr, 1947) connecting the outermost location points is the least conservative method, and it incorporates areas in which individual animals never were seen. The habitat type minimum area method is based on my analysis of the plant community boundaries and on the locations for an individual animal in relationship to those boundaries. Instead of connecting the outermost location points with straight lines, I followed the boundaries of the plant communities in which the movements occurred. I believe this method is a more accurate determination of the size and shape of the home range area because my data from the intensive radio-tracking study indicate that individual porcupines remain closely associated with particular plant communities. This method is similar to the atypical-habitat elimination method of Ables (1969).

TABLE 2. Home range variables for six porcupines in northeastern Oregon.

	1	2	3	4	5	6
Age	Juv.	Adult	Adult	Adult	Adult	Adult
Sex	Male	Female	Female	Female	Female	Female
Date instrumented	10 Jan 74	2 Feb 74	22 Feb 74	5 Apr 74	5 May 74	8 Jun 74
Date radio package removed	31 Jan 74	6 Mar 74	7 Jul 74	27 Aug 74	27 Aug 74	27 Aug 74
Number of days instrumented	22	33	136	145	115	81
Area in hectares						
Minimum area (Mohr, 1947)	3.9	8.1	28.8	80.8	82.1	22.6
Modified minimum (Harvey and Barbour, 1965)	a	a	a	39.1	66.8	a
Circle from mean activity radii (Dice and Clark, 1953)	3.1	13.8	19.5	23.0	65.6	17.1
Habitat type minimum area	a	a	a	62.5	77.8	15.4
Distance in meters						
Maximum length	274	399	747	1241	1463	792
Maximum width	174	337	671	937	722	512

a—unable to calculate

Porcupine No. 1 used an area of 3.9 ha during three weeks in January and porcupine No. 2 used 8.1 ha in February. In January and February movements were short and the animals often remained stationary for several days. No. 3 was radio-tracked from late February through early May. During this period weather conditions improved and porcupine movements increased. No. 4 and No. 5 were instrumented in the spring season and they demonstrated the trend toward a further increase in home range area into the summer season. Their cumulative home range sizes were likely at or near maximum size. Although radio-tracking was halted at the end of August, ranges would not have in-

creased appreciably before cold weather decreased overall movements. No. 6 was tracked from June through August. Her movements tended to be shorter than those of either No. 4 or No. 5 for the same period. All three females had young; however, the fate of the offspring of No. 4 and No. 5 was unknown. The young of No. 6 could be found close to its dam throughout the summer. The young tended to move in loose association with its dam and often the two were separated by only a short distance. Similar behavior was reported by Marshall *et al.* (1962).

Porcupine recaptures along a 7.6 km route aided in the determination of home range size. The maximum distances between captures for 51 porcupines recaptured along the route (total of 112 recaptures) are summarized in Table 3. The range in average maximum distance between summer captures of 525-1156 m (Table 3) compares closely to the range of 512-1463 m (Table 2) for the maximum width and length of home ranges determined by radio-tracking during spring and summer.

TABLE 3. Average maximum distance (m) between summer captures for 51 porcupines along a 7.6 km route in northeastern Oregon.

Number of captures/ animal	Number of animals in sample	Average maximum distance between captures	Extremes of average maximum distance between captures
2	26	525	0-2119
3	11	858	337-2131
4	4	662	369-1188
5	4	1131	546-1717
6	2	802	642-1173
7	3	1140	385-2632
9	1	1156	

These movement data appear very similar to those recorded by Dodge and Barnes (1975), but larger than those reported in most other studies. Dodge and Barnes (1975), in a western Washington Douglas-fir forest, found an average daily movement of 273 m and an average range of 81.2 ha (minimum area method) for females radio-tracked 10 to 13 months. This finding is similar to the yearly average movement of 238 m and to the 80.8 and 82.1 ha ranges for porcupines No. 4 and No. 5, respectively, which I tracked in northeastern Oregon. Brander (1973) reported an average summer daily movement of 150 m; Marshall *et al.* (1962) reported average movements during late May through early July of 111 m and 129 m, from dusk to dawn, and 81 m and 80 m, from dawn to dusk, for two adult females. These movements for porcupines in Michigan hardwood-hemlock forests were much less than those I found in Oregon. The average distance of 446 m between captures for summer months reported by Randall (1971) in mixed shrub-pine vegetation in Nevada was smaller than that within my study area (Table 3). In a pine-juniper forest in northern California, Hoffer (pers. comm.) found an average summer movement of 144 m. He believed reduced movement occurred because animals were feeding in alfalfa fields. His figures for winter months (65 m) are similar to those I found.

Porcupine movements apparently are influenced strongly by habitat and vary from one area to another. Porcupines in eastern and midwestern hardwood-hemlock forest appear to occupy separate summer and winter ranges and tend to concentrate at denning

areas or areas of prime habitat (Dodge, 1967). Winter movements are reduced; animals only leave the shelter of dens to feed in nearby trees. Shapiro (1949) reported an average distance of 131 m between captures in New York, and Dodge (1949) reported 91 m in Massachusetts. Krefting *et al.* (1962) in Wisconsin found an average of 829 m between summer captures and winter recaptures. Dodge (1967) found six animals traveled an average of 1500 m from winter captures to summer recaptures. Such seasonal shifts in home range did not occur in my study area. Similar findings were reported by Dodge and Barnes (1975), Hoffer (1967), and Randall (1971) in other western forests.

Porcupines appear to maintain home range areas in successive years. Ten animals tagged the summer of 1973 and recaptured the summer of 1974 in this study had maximum distances between captures averaging only 722 m (Table 4). Similar results have been found in other studies. Krefting *et al.* (1962) recaptured two animals, tagged two years previously at winter feeding areas, an average distance of 100 m from their original capture sites. Randall (1971) had an average recapture distance of 536 m for 12 porcupines captured one summer and recaptured the next. Brander (1973) found an average distance of 699 m between capture sites for four porcupines recaptured after 1-10 years.

TABLE 4. Ten porcupines captured the summer of 1973 and recaptured the summer of 1974 along a 7.6 km route in northeastern Oregon.

Animal number	Original capture date	Days since 1st capture	Number of captures/ animal	Maximum distance between captures (m)
7	7 Aug 73	382	4	369
8	15 Aug 73	334	2	449
9	16 Aug 73	369	4	722
10	16 Aug 73	343	2	353
11	19 Aug 73	315	2	0
12	19 Aug 73	346	2	369
13	21 Aug 73	313	2	225
14	25 Aug 73	310	2	449
15	28 Aug 73	374	7	2632
16	3 Sep 73	355	3	1653

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Douglas-fir Tussock Moth Egg Hatch and Larval Movement from Egg Masses in Central British Columbia

Abstract

Patterns of Douglas-fir tussock moth (*Orgyia pseudotsugata* McD) egg hatch and movement of larvae from egg masses were studied at a site near Heffley Creek, 25 km north of Kamloops, British Columbia, in June 1975. A majority of the eggs (65 percent) hatched between 0800 and 1600 hours (PST) and 45.8 percent hatched between 0800 and 1200. Egg hatching was complete in nine days. Peak hatch occurred after four days, and peak movement of larvae from the egg masses occurred three days later. Patterns of larval movement from the egg masses during the day were similar to egg hatching patterns. Average percent eclosion of eggs was 20.5 percent. Cumulative egg hatch at the British Columbia site was reasonably well predicted with the equation $y = -88.78 + 97.45 \log x$, where y = cumulative percentage hatch, and x = cumulative degree days after hatch initiation above a base of 5.6°C. The model was constructed using independent data from California and Oregon.

Introduction

The Douglas-fir tussock moth (*Orgyia pseudotsugata* McD), a univoltine insect, defoliates true firs (*Abies* spp.) and Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) in western North America (Wickman *et al.*, 1973). Defoliated trees may be killed outright or top-killed with resulting loss of growth.

Egg hatching has been studied by Cameron (1970) and Edwards (1965) in the laboratory and by Wickman (1976 a and b) in the field in California and Oregon, respectively. The objectives of this study were to (1) study patterns of egg hatching and larval movement from the egg masses at a field site in British Columbia, (2) study egg viability, and (3) develop a predictive model for egg hatching.

Methods

Study Site

The study site was located approximately 25 km north of Kamloops, British Columbia, near Heffley Creek at an elevation of approximately 750 m. Dominant vegetation was Douglas-fir and ponderosa pine (*Pinus ponderosa* Laws.), and the trees were widely spaced. The Douglas-fir trees were extensively defoliated in 1974 and large numbers of egg masses were present in the tree canopies. The study was conducted from 2 to 13 June 1975.

Egg Hatching

Egg masses were collected from small trees and the lower branches of large trees. Hatch was observed on 25 masses set approximately 1.5 m from the forest floor on a tree. The egg masses were glued to paper on a 5 x 5 grid, 10 cm apart. Egg masses faced south and east. Egg hatch was also observed on 25 egg masses on paper laid on the forest floor using the same grid pattern. Larvae were removed with tweezers each hour from

0800 to 1600 hours (PST). Hatching was also studied in the period from 1600 to 0800 hours.

Larval Movement from Egg Masses

The number of larvae moving from 31 egg masses on the tree and 20 egg masses on the forest floor was studied hourly each day from 0800 to 1600 hours and from 1600 to 0800 hours. Egg masses were glued to paper as they were in the hatching observations. A larva was considered to have left an egg mass when it moved more than 1.5 cm from the edge of the egg mass.

Egg Viability

The total number of eggs in each egg mass was recorded in both the hatching and dispersing observations in order to ascertain egg viability. Percent eclosion was ascertained as (no. of eggs hatched/total no. of eggs) x 100.

Temperature Data

Temperature data were obtained from hygrothermograph (Casella) set in a clearing approximately 100 m from the specific study site. Degree day determinations were calculated using average daily temperatures and a base of 5.6°C (42°F). This threshold temperature was suggested by Wickman (1976 a and b).

Results and Discussion

Pattern of Egg Hatching throughout the Day

Table 1 shows egg hatching patterns observed during the day. For combined egg masses on the tree and forest floor, 35 percent of the eggs hatched between 1600 and 0800 hours and 65 percent of the eggs hatched from 0800 to 1600 hours. Thus a majority of the eggs hatched during daylight hours, in general before noon; 45.8 percent hatched between 0800 and 1200 hours. There appeared to be a slight afternoon peak between 1300 and 1400 hours for the eggs on the tree, but hatching patterns on the tree and forest floor were not vastly different.

TABLE 1. Average percentage of eggs hatching from egg masses on the tree and forest floor and combined tree and forest floor egg hatch each hour from 0800 to 1600 and from 1600 to 0800 from 3 to 12 June 1975.

Time of Day (PST)	Percentage Hatch		
	Egg Masses on Tree	Egg Masses on Forest Floor	Combined Forest Floor and Tree Egg Masses
1600-0800	35.1	35.4	35.0
0800-0900	17.8	27.3	24.0
0900-1000	14.8	5.9	8.8
1000-1100	4.3	8.1	6.9
1100-1200	5.6	6.3	6.1
1200-1300	8.0	6.6	7.1
1300-1400	12.4	4.8	7.3
1400-1500	2.0	5.6	4.8
1500-1600	0.0	0.0	0.0

In a laboratory study in British Columbia by Edwards (1965), 90 percent of egg hatching occurred between 0600 and 1800 hours, 65 percent occurred between 0600

and 1200 hours, but no hatching occurred between 2400 and 0600 hours. This pattern of hatching contrasts with that found in a similar laboratory study in California by Cameron (1970), who found that egg hatch was evenly distributed throughout the day. Fifty-eight percent of the eggs hatched from 0600 to 1800 hours at 24°C, and there was considerable hatching (18 percent) between 2400 and 0600. Unfortunately, egg hatch was not observed at the study site from midnight to 0600 hours; thus, there is no way to tell which laboratory study the field hatching patterns most closely resemble.

Length of Egg Hatching Period

Hatching commenced on 3 June for both sets of egg masses and was complete by 11 June (9 days) on the tree (Figure 1a) and on the forest floor (Figure 1b). Further south in Oregon in 1973, Wickman (1976b) found hatch periods in the field ranging from 7 to 14 days. Hatch periods in California in 1972 were about 10 days (Wickman, 1976a). The period from initiation to end of hatching thus was similar at the California, Oregon, and British Columbia sites.

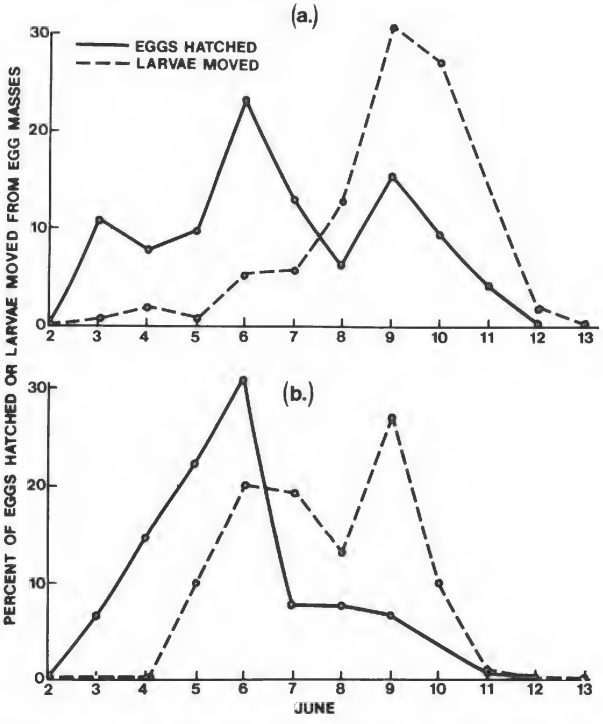

Figure 1. Percentage of eggs hatched and larvae dispersed from egg masses on (a) the tree and (b) the forest floor from 2 to 13 June 1975.

Maximum egg hatch was recorded on the fourth day after hatch initiation on both sets of egg masses (Figure 1). Similar results for the time of maximum hatching were found by Wickman (1976a) in California (2-4 days after initiation). In Oregon, however, maximum hatching occurred from 4 days to 10 days after initiation (Wickman,

1976b), and at one site hatching was bimodal with peaks at 3 and 10 days.

Movement of Larvae from Egg Masses

For the combined egg masses on the forest floor and tree the pattern of movement of larvae from the egg masses during the day (Table 2) resembled egg hatching patterns (Table 1). Between 1600 and 0800 hours, 37.6 percent of the larvae left the egg masses, 62.4 percent left between 0800 and 1600 hours, and 47.7 percent left between 0800 and 1200 hours (Table 2). Considerably more larvae moved from the egg masses on the tree before 0900 hours (69.6 percent) than from the egg masses on the ground (38.3 percent), perhaps reflecting slight differences in microclimate, especially exposure to radiation.

TABLE 2. Average percentage of larvae moving from egg masses on the tree and forest floor and movement from combined tree and forest floor egg masses from 0800 to 1600 and 1600 to 0800 from 3 to 13 June 1975.

Time of Day (PST)	Percentage of larvae moved from egg masses		
	Egg Masses on Tree	Egg Masses on Forest Floor	Combined Forest Floor and Tree Egg Masses
1600-0800	43.9	12.8	37.6
0800-0900	25.7	25.5	25.7
0900-1000	6.8	19.7	9.4
1000-1100	5.9	16.0	7.9
1100-1200	4.0	7.3	4.7
1200-1300	4.9	13.1	6.6
1300-1400	4.3	3.6	4.2
1400-1500	4.5	1.8	3.9
1500-1600	0.0	0.0	0.0

Figure 1 shows that while peak egg hatch occurred on 6 June, peak movement of larvae from the egg masses occurred three days later on 9 June from egg masses on both the tree and forest floor. This finding is similar to the situation found in California (Wickman, 1976a) and Oregon (Wickman, 1976b).

Egg Viability

Percent eclosion was 17 percent (461/2717) and 24 percent (1074/4461) for the eggs on the tree used for the hatching and larval movement observations, respectively. Of the eggs on the forest floor, 28 percent (937/3329) of those used for hatching observations hatched, but only 13 percent (274/2063) of those used for movement observations hatched. Average percent eclosion was 20.5 percent.

This low value for percent eclosion is probably related to the length and temperature of the exposure period after the eggs were laid. Cameron (1970) found under laboratory conditions that long periods of egg exposure to cold storage periods resulted in a decrease in percent eclosion. He found eclosion to be 48 percent following 67 days exposure to temperatures of approximately 3°C, but this figure fell to about 20 percent after 147 days, and to 12 percent after 186 days. No larvae hatched after storage for 360 days. Assuming that eggs in the field in British Columbia were exposed to approximately 170 days of average temperatures <3°C (from Kamloops Airport weather data), then the field and laboratory data match.

Prediction of Egg Hatching

The predictive model was constructed using the basic premise that cumulative hatch is determined by degree day accumulations after hatch initiation regardless of the location; i.e., throughout the range of the Douglas-fir tussock moth. Hatch data from California (Wickman, 1976a) and Oregon (Wickman, 1976b) were used along with degree day determinations, to construct a semilogarithmic linear regression model of the form:

$$y = a + b \quad \log x$$

where y = cumulative percentage hatch,

x = degree day accumulations after hatch initiation above a base of 5.6°C, and a and b are the usual constants.

The following model equation resulted:

$$y = -88.78 + 97.45 \quad \log x$$

The correlation coefficient for this regression was $r = 0.7836$ (significant at the 99 percent level, $n = 23$) and $r^2 = 0.6140$. Observed versus predicted values in Figure 2 show that this model predicts cumulative hatch rather well. Thus the model assumption is apparently reasonable.

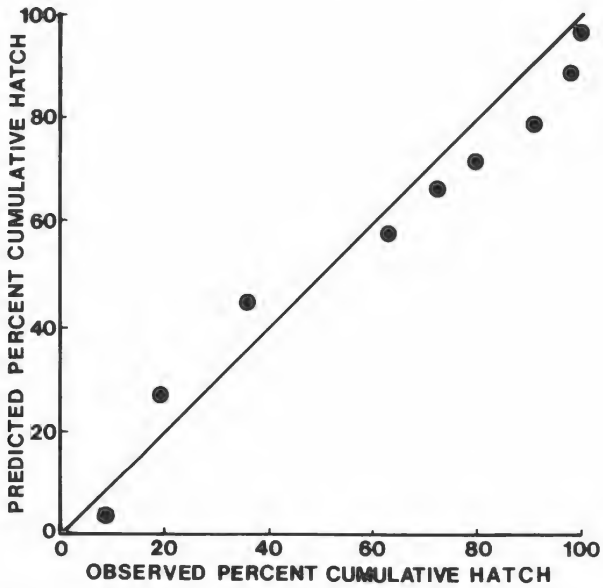

Figure 2. Observed cumulative percentage egg hatch at the British Columbia site versus predicted cumulative percentage egg hatch based on the equation $y = -88.78 + 97.45 \log x$, where y = cumulative percentage hatch, and x = cumulative degree days after hatch initiation above a base of 5.6°C. Solid line indicates perfect agreement.

Using the Kamloops data alone, however, the relationship between cumulative percentage hatch and log degree day accumulation was even better, giving $r = 0.9787$ (significant at the 99% level, $n = 9$) and $r^2 = 0.9579$ for $y = -104.42 + 111.13 \log x$. This finding perhaps indicates the closer relationship between the hatch location and the location of the temperature sensor at the British Columbia site.

Summary and Conclusion

A majority of the eggs (65 percent) at the British Columbia site hatched between 0800 and 1600 hours and 45.8 percent hatched between 0800 and 1200 hours. Egg hatch was complete in nine days, which is similar to that found in California and Oregon. Maximum egg hatch was recorded on the fourth day, and peak movement of larvae from egg masses occurred three days later. The pattern of larval movement during the day was similar to the egg hatching pattern in that 62.4 percent of the larvae left the egg masses between 0800 and 1600 hours and 47.7 percent left between 0800 and 1200 hours. Average percent eclosion was 20.5 percent.

Cumulative egg hatch at the British Columbia site was predicted reasonably well using the regression model $y = -88.78 + 97.45 \log x$ where $y =$ cumulative percentage hatch, and $x =$ degree day accumulations after hatch initiation above a base of 5.6°C.

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Germination in Black Greasewood (Sarcobatus vermiculatus (Hook.) Torr.)

Abstract

Greasewood (*Sarcobatus vermiculatus* (Hook.) Torr.) is an indigenous spiny shrub found on moist alkali-sodic soils in southeastern Montana. Flowering is primarily in August, seed matures in October, and seed shatter begins in November. Filled seed percentages ranged from 16 to 94. Highly viable dewinged seed numbered 425 per gm. When the membranous pericarp is ruptured, germination—a simple uncoiling of the embryo—may occur in less than an hour and root hairs may appear in less than 24 hours. Rapid imbibition occurs when the pericarp is fully intact; however, germination is slow and many achenes do not germinate even after 30 days of being fully imbibed. Germination peak was in two days, and germination was 98 percent complete in ten days. Optimum germination temperatures were 4°C and 10°C without stratification, and either 30°C or alternating temperatures when preceded by stratification.

Introduction

Black greasewood or greasewood is a spiny, erect shrub 1-2 m in height (Booth and Wright, 1966). The species is distributed throughout most of the western states on heavier soils which receive either surface or subsurface moisture from higher areas. Clements (1916) described greasewood communities as being stable due to excess salts, relying on water tables, and having soil surfaces that frequently dry out during summer. This water table may be up to 6 m deep (Rollins *et al.*, 1968).

Soils on which the species grow tend to be clay-loams, silt-loams, or deep fine sandy loams; these soils are most likely alkali-sodic in the upper stratum immediately under the plant crown, and either saline or alkali-sodic between plants and in the strata below a depth of 23-30 cm (Brown, 1965; Fireman and Hayward, 1952; Richard, 1965a, 1965b; and Richard and Cline, 1965). Greasewood concentrates exchangeable sodium in the surface horizon underneath the canopy (Richard and Cline, 1965), and this concentration is directly related to canopy size. Soils supporting greasewood can have exchangeable sodium as high as 12.0 meq/100 gms (Brown, 1965) and pH as high as 9.83 (Fireman and Hayward, 1952).

The forage value of the plant varies by area and animal species. It is reported as good browse for deer and antelope, and it is occasionally browsed by cattle (Morris *et al.*, 1962); it is considered poisonous to sheep under conditions of high, rapid intake because of its oxalate production (MacLean and Davidson, 1970).

Greasewood concentrates sodium in the upper soil horizons, appears to be a stable dominant under moist-sodic conditions, and occurs widely in the Fort Union Basin of southeastern Montana. It is important to understand its ecological significance within the plant community and its response to reclamation and rehabilitation practices of large expanses of disturbed lands resulting from coal strip mines. This paper examines some of the aspects of plant establishment (particularly germination) that should aid in

determining the plant's ecological requirements and response within the natural community, as well as its response to perturbations within that community. Germination studies have not previously been reported.

Methods and Materials

Seeds from greasewood were collected in 1975 and 1976 near Epsie, Montana, on an upland bench in the mixed-prairie, and in 1975 from the Tongue River bottoms south of Birney, Montana. Collection was by hand stripping in late October and November of 1975 and late September of 1976. Seeds were dried under cool conditions, the wings removed from the dried seed by a mechanical flail, hand screened, and stored in the laboratory in paper envelopes at 21°C and 20 percent relative humidity.

Seed fill determinations were made from ten samples of ten seeds each, and from analysis of ungerminated seeds in the germination trials. Five random samples of 100 seeds each were weighed to obtain seed number per unit weight and two samples of 13 cm^3 each were used to estimate weight-volume relationships.

Seeds were dusted with captan, placed directly on moist pure cellulose pads in covered petri dishes, and germinated under controlled temperature and light conditions. Four replications of 25 seeds each were examined under each treatment. Germination counts were made daily for 30 days. Seeds were considered germinated when the radicle protruded 5 mm or more. The stratification treatment, when applied, consisted of placing the seeds on moist cellulose pads within a 4°C dark cabinet for 30, 60, and 90 days.

Germination was conducted at 10, 20, and 30°C constant temperature, and at 20-5°C and 30-20°C day-night alternating temperatures. Light exposure treatments were dark, 8 hours light, and 14 hours light.

Observations were made on seed and seedling morphology, and the effect of freezing on imbibed embryos.

Phenology observations in the general area of seed collection were made in 1975 to determine seed ripe and seed shatter dates.

Results

In southeastern Montana pistillate flowers were found from late July to late August in 1975. Seed set began in mid-August, mature seeds appeared in late September, and all seeds were mature by early November, at which time seed shatter began. A few seeds produced in 1974 were found intact in July of 1975, so seed shatter appears to be a slow process.

The greasewood fruit is a circular, winged, coriaceous utricle containing an achene composed of a transparent membrane (pericarp) which surrounds a helically coiled embryo (Figs. 1 and 2). No endosperm is present. The embryo coil contains the two cotyledons innermost, successively followed by the hypocotyl and the radicle. Both the cotyledons and hypocotyl are chlorophyllous at seed maturity.

In the germination studies the percentage of filled seed became very important, inasmuch as it varied from 16 to 94 percent (Table 1). Insect damage was particularly high—58 percent—in the 1976 collection from Epsie. Using a seed blower eliminated nearly all damaged, undeveloped, and empty seeds from the trials.

Weight of dewinged seed proved to be the best measure of seed quality. Dewinged seed from Epsie and Birney collections from which empty seed had been removed by

Figure 1. Winged utricle of greasewood (scale in mm).

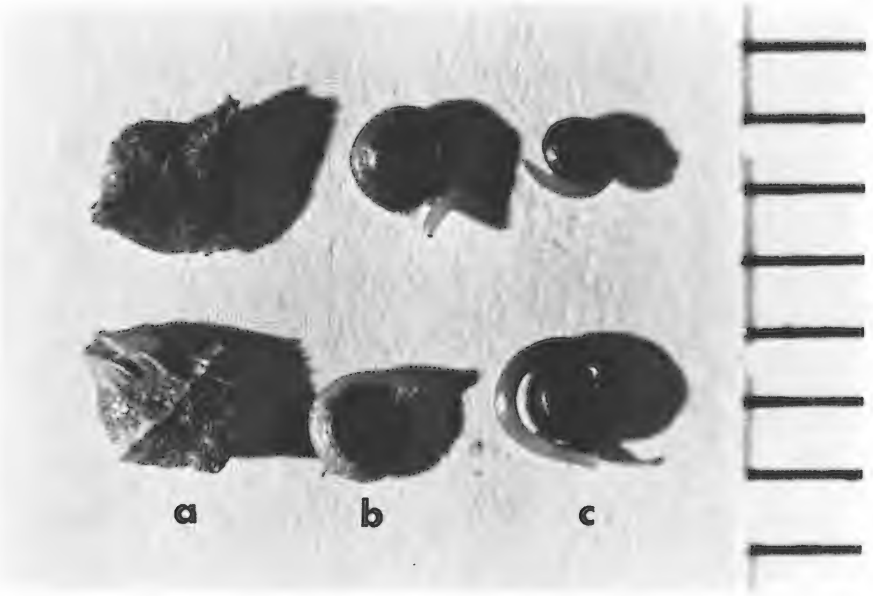

Figure 2. a) Dewinged greasewood utricle, b) pericarps intact, and c) the helically coiled embryo (scale in mm).

a seed blower yielded 425 and 435 seeds per gm, respectively (coefficient variation—CV = 2 percent and 1 percent, respectively). Random samples from dewinged seed of the Epsie-76 collection yielded 775 seeds per gm (CV = 5 percent). Filled dewinged seed from the Birney collection averaged 606 gm per liter, while dewinged seed from the total population in the Epsie-76 collection averaged 202 gm per liter.

TABLE 1. Characteristics of greasewood seed collected in 1975 at Epsie and Birney and in 1976 at Epsie (s=standard deviation).

Collection	Filled		Insect Damaged		Empty	
	%	s	%	s	%	s
Epsie-75	70	15.6	16	7.0	14	14.3
Birney-75	94	7.0	1	3.2	6	7.0
Epsie-76	16	9.7	58	14.8	26	13.5

The germination process is one of rapid imbibition by the pericarp and embryo; if the pericarp is ruptured or weak in any area, the imbibition is followed by an immediate uncoiling and extension of the radicle, hypocotyl, and finally the cotyledons (Fig 2). The radicles on many seeds from the Epsie-75 collection were protruding before they could be placed in the germinator and some seedlings were fully formed in an hour.

Root hairs appear early, on some seedlings within 24 hours. Radicle elongation precedes cotyledon elongation, and the cotyledons remain partially coiled up to an average radicle length of 25 mm. Radicle elongation depends on contact with substrate; in this study it averaged 10 mm/24 hr for the first five days at optimal temperatures.

The Birney-75 collection responded by rapid imbibition of the embryo and pericarp; nonetheless, the pericarp did not rupture, and although it maintained a positive pressure inside, the embryo did not emerge. This turgid, fully imbibed condition lasted the full 30 days on many seeds. Rupture of the membrane with a needle caused a rapid expansion of the embryo.

Germination energy was high for both the Birney-75 and the Epsie-75 and -76 collections. A majority (60 percent) of the trials reached a peak germination rate in two days. Sixty-seven percent (s=2.1) of all seed had completed germination at the end of two days. A ten-day cut-off point in germination counting is suitable since no seed germinated after this point in 41 percent of the trials, and the mean germination after 10 days for all trials was 1.8 percent (s=2.2) of the total final germination.

Optimum germination temperatures were cool (10°C) without stratification, and warm (20-30°C) with stratification (Table 2). A period of cool, moist stratification reduced germination percentage and rate when followed by temperatures below 20°C. Data show that stratification is neither required for high germination nor does it necessarily inhibit germination.

The only significant difference in light and dark germination was a reduction at warm (30°C) temperatures under dark conditions.

A period of after-ripening is apparently necessary for the embryo to mature. This time required for maturation ranges from a minimum of 30 days to a maximum of 60 days under dry conditions. Immediate germination of seed, without an after-ripening period, never exceeded 24 percent.

Germination response also changed with longer periods of after-ripening. Percent germination at low temperatures improved significantly (P=.90) as seed age increased. Following 90, 180, and 300 days of dry storage, germination at 4°C dark was 43, 57, and 93 percent, respectively.

TABLE 2. Germination percent of greasewood seed based on pure, live seed—Epsie-75 and -76 collections.

		Temperature (°C)					
		Constant				Alternating	
	Light Hours	4	10	20	30	20-5	30-20
UNSTRATIFIED							
	Dark-0	**79a***	**100ab****	89ac	61ad	—	—
	8	—	**87a**	79a	86a	—	—
STRATIFIED							
30 day	14	—	63a	71bd	**96ce**	76bde	**94cde**
60 day	14	—	64a	89bd	**100cde**	**100cde**	**100cde**
90 day	14	—	60ab	79ab	84bc	96d	**100e**

*Optimum germination, numbers in bold face not significantly different (P=.90) from maximum.
**Row means not followed by the same letter are significantly different (P=.90), as determined by pair-wise sample t test.

Rate of germination reached a maximum following 60 days of storage. Two days were required to reach 50 percent of total germination with no differences existing in the 10-30°C range, or between light and dark treatments. As with total germination, the rate appears much slower for freshly collected seed, and it appears to be directly related to temperature.

Seed from the Birney collection germinated at about the same rate as that of the Epsie collections. Although the Birney seed averaged lower total germination, the difference was significant only at 30°C temperature (86 vs. 66 percent). The major difference in the two collections was the retained viability of the ungerminated seed from the Birney collection, while ungerminated seeds from the Epsie collections had all lost their viability at the end of 30 days.

Since the breakdown of the pericarp is necessary for germination, freeze-thaw action was examined for indications of response. Following the 30-day germination trial, two samples from the Birney collection containing 10 germinated seedlings and 15 fully turgid embryos still surrounded with the pericarp were placed in a freezer (-10°C), one for 24 hours and one for four days, after which they were exposed to 20°C temperature and eight hours of light. The short freeze stimulated all imbibed embryos to germinate and did not damage previously emerged seedlings. The longer freeze period killed all previously emerged seedlings, but again the imbibed embryos germinated when placed in the warmer environment.

Discussion

Black greasewood in southeastern Montana begins to form mature seeds by late September. Following an after-ripening period of 30-60 days, germination is high at either high or low temperatures, although there is an increase in the ability of seeds to germinate at very low temperatures with longer after-ripening periods.

Germination from pure, live seed should exceed 60 percent under optimal conditions. Germination and seedling growth are both very rapid from embryos not sur-

rounded by a resistant pericarp, while germination is slowed or delayed for embryos surrounded by a resistant pericarp unless, as indicated above, freeze-thaw action breaks the membrane down. Observations made on the two populations suggest the presence of a chemical inhibitor to germination in the Birney collection which at least slows germination in 25 percent or more of the population. Although this inhibitor may be present in the Epsie population, the membranous pericarp is not continuous around the embryo, and thereby allows unrestricted embryo expansion. Seeds from both populations would be expected to germinate differently under natural conditions. Fall germination should occur in both; however, the Birney source possesses a delay mechanism for a portion of the seed. High seedling mortality would be expected on a site where freeze-thaw action occurs, for example, on southerly aspects.

Seed dispersal from the plant is a gradual process occurring throughout the late fall, winter, and spring, therefore presenting a multitude of conditions for germination. Although all indications are that greasewood should be quite competitive in reproducing itself, established seedlings were infrequent at the two collection sites. Since the species is long-lived and produces abundant seed, maintenance in the community seems assured. Regeneration, however, would be strongly reduced by insect-caused seed damage as shown in the 58 percent embryo loss of the 1976 Epsie collection and by freeze-injury to new seedlings.

Acknowledgments

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Association News

The Annual Meeting of the Association will be held 27-29 March 1980 at the University of Idaho in Moscow. Dr. Doyle Anderegg, Program Chairman, has announced that the first call for papers will be mailed November, 1979. The deadline for submission of abstracts is 9 January 1980. The section chairmen are:

Botany	Douglas Henderson
Forestry	Charles Hatch
Geology	Peter Isaacson
Science Education and Math	Michael Heikkinen
Chemistry and Physics	
Social Sciences	Eric Jensen
Soil and Water	Maynard Fosberg
Zoology	Don Johnson

Contributed paper sessions will meet in the University of Idaho Student Union; the annual banquet is planned for the new University Inn.

The annual fall meeting of Officers and Trustees was held in Ellensburg, Washington, 27 October 1979. Reports were presented by the Secretary, Treasurer, Editor, and Committee Chairmen. The Treasurer reported that the Association is in relatively good financial condition: much of the credit for the current financial status must go to Bob Christman and Dan Guthrie at Western Washington University for their handling of the 1979 Annual Meeting.

The Trustees again approved a $2 late dues charge for 1980 dues paid after 15 January 1980. A total of $400 has been allocated by the Trustees for research grant awards to be given to at least two applicants at the 1980 Annual Meeting. Information and proposal guidelines may be requested from:

Dr. L. M. Lavkulich
Department of Soil Science
University of British Columbia
Vancouver, B. C.
Canada V6T 1W5

Editor Don Satterlund reported that the backlog of accepted papers for Northwest Science is declining: the time lapse between acceptance and publication is approximately 15 months. To counter the imbalance of subject material currently received by the Editor, the Trustees directed that the Editor include a paper from every section within each issue of Northwest Science regardless of acceptance date. This policy will be effective for all papers accepted after 27 October 1979.

In addition, the Trustees agreed to the following changes in reprint and page charges for Northwest Science effective for all papers printed after January 1980:

No. of printed pages	1-4	5-8	9-12	13-16	17-20
Cost per 100 copies	$30	$40	$50	$55	$65

Reprints are sold in units of 100 at the above price. Covers are $30 per 100 copies additional.

Page charges will increase to $35 per page.

William R. Rayburn, Secretary

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